AVIAN TAXONOMY FROM LINNAEUS TO DNA

PAPERS PRESENTED AT A JOINT MEETING BETWEEN THE BRITISH ORNITHOLOGISTS' CLUB AND THE LINNEAN SOCIETY OF LONDON HELD AT BURLINGTON HOUSE, 23 MARCH 1996

PREFACE

by Robert A. Cheke

The use of the binomial system to classify plants and animals, as formalised by Linnaeus, continues to be the means by which species are named. Acceptance of binomials after much controversy was followed by further, often heated, debates about the usefulness of the trinomial system and the idea of subspecies. The latter arguments occupied the members of the British Ornithologists' Club (BOC) for many years, especially at the end of the 19th century. We have now come full circle and, once again, the subspecies concept is under criticism, but mostly for quite different reasons from those advanced by the contemporaries of the founders of the BOC. It is salutary that there is probably now more disagreement over what is meant by species than there has ever been (Malliet 1995).

The purpose of the gathering, fittingly held in the meeting rooms of the Linnean Society of London, was to provide an opportunity to discuss modern views of avian taxonomy, at the same time remembering the historical context. The papers from the meeting which are published in full here are only those which addressed species concepts *per se*. Abstracts are included for three of the others, as well as a paper on Linnaeus' correspondence with Scopoli, based on a poster presentation.

Current arguments are not without practical import, and the consequences that their resolution might have, for purposes such as conservation or zoo-archaeology, was another major issue for discussion, as was the whole construct of traditional classification. If a population is genetically distinct, such as one of the groups of Red Kite *Milvus milvus* described by Parkin, why shouldn't it be classed as a subspecies or even a species? Indeed, where can the line be drawn, since each individual bird has a unique genetic code? Does the logic necessitate the acceptance of many more species of birds than are hitherto recognised? Are traditional higher order groupings redundant?

As Jeremy Greenwood points out in the introductory contribution, there are many taxa of taxonomic thought and each might classify the same group of animals differently. The abolition of subspecies is one consequence of the phylogenetic species concept (PSC) advocated by Robert Zink, whose conclusions would have been heard with approval by some of the BOC's founders, as well as by a few of the Italian ornithologists discussed by Violani and Barbagli. Zink's arguments include conclusions derived from DNA data and analyses which would be difficult to obtain without the use of microprocessors. Although the post-Watson and Crick era has seen extraordinary advances in our understanding of biological processes at the molecular level, especially when coupled with information technology, DNA may yet only serve taxonomy as another set of "characters", so far as bird classifications are concerned. David Snow maintains support for the biological species concept and warns that the general adoption of the PSC could lead to decades of instability in taxonomy. He also draws attention to the proliferation of new species (though this in itself is not a valid argument against the PSC), which adherence to the adoption of the PSC would engender; and these two themes are taken up by Collar, who emphasises that the adoption of the PSC would make the role of international conservationists impossibly difficult. The 'problem' of the recognition of extra species, under the PSC, was emphasised in an account of the meeting (Martin 1996) but disputed by Zink (1996), who pointed out that most of the putative extra species are already recognised as subspecies.

Parkin demonstrated that there are genetic differences between populations of Red Kites from Germany, Spain and Wales, the latter being the least variable and having the poorest breeding success. Russell showed that it is possible to identify mummified birds of prey from X-rays, using taxonomic methods of much newer vintage than the mummies. The main conclusions reached in a study of eggshell structure to elucidate taxonomic relationships, principally at levels above the species (mainly sub-order or order), were summarised by Mikhailov. A detailed account of this research will appear elsewhere (Mikhailov 1997).

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Introduction: the diversity of taxonomies

by *Jeremy J. D. Greenwood*

Taxonomy and related fields are battle grounds onto which the non-combatant ventures at his peril, liable to be shot at from all sides. Even the definition of the subject is one on which its practitioners clearly disagree. I shall accept that: "Taxonomy is, strictly speaking, the study of the principles and practice of classification" (Jeffrey 1977). Classifications have three main uses in biology: they allow us to summarise and organise our knowledge about living organisms, they help us to identify organisms, and they can provide an approximate summary of evolutionary relationships. The first is important because of the sheer diversity of living organisms and the second because that diversity makes identification difficult. Summarising evolutionary relationships is important because "Nothing in biology makes sense except in the light of evolution" (Dobzhansky 1973). So most biologists use classifications in most of their work. One might therefore assume that taxonomy would be a key element in the education of young biologists. In Britain, at least, this assumption would be completely unjustified; without having carried out any systematic investigation, I suspect that most undergraduate courses are devoid of formal teaching in taxonomy. As a result, most of us have a rather hazy knowledge of the principles and methods underlying classifications; even worse, because we use classifications every day of our lives, we may be unaware of quite how hazy our knowledge is. Furthermore, Arthur Cain's (1959) prescient opinion that "we are about to see a considerable revision of the whole basis of taxonomic theory" has been amply justified; with the major developments in taxonomic philosophy, in sources of data, and in analytical methods that have occurred in the last four decades, the gap between the taxonomist and the users of the taxonomists' products may, indeed, be wider than ever before. For that reason, I shall take some space to look at those developments, in the hope that my brief summary may be of use to others who feel the need to be more familiar with modern ideas in taxonomy but whose work, like mine, has prevented them from closely following those ideas as they have developed. My own recent education in the subject has relied particularly on: Ridley (1986), who provides a thought-provoking, if personal, view of the major schools of taxonomy from the point of view of an evolutionary biologist rather than of a practising taxonomist; Forey *et al.* (1992), who clearly explain cladistic views and methods; and Hillis & Moritz (1990), who cover many of the principles as well as covering in detail how molecular evidence may be used. (For those whose knowledge of molecular evolution is becoming rather rusty, Li & Graur (1991) provide a useful introduction to current ideas.)

Organising knowledge

We are able to use classification as a means of organising knowledge about living organisms particularly because species fall into clusters.

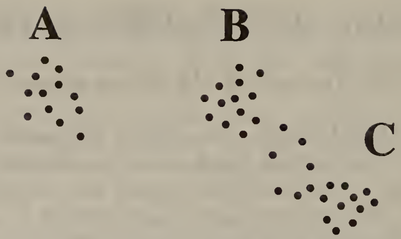

Figure 1. Clusters of species in a two-dimensional character space. Cluster A is distinct but do B and C represent one cluster or two? If they form two clusters, where should the dividing line be drawn?

For example: bird species share certain characteristics in common, mammal species share other characteristics, and there is a gap between them; bats share some characteristics with birds but are still firmly linked to the mammals by most of their characteristics; bats do not cause us to have difficulty in recognising the two chief clusters of warm-blooded vertebrates or in distinguishing between them. We can make general statements about all members of such clusters, to help us reduce our knowledge base to manageable proportions. The process is further facilitated by the fact that we may arrange the clusters in a non-overlapping hierarchy, with clusters at each taxonomic level themselves being clustered at the level above. Unfortunately, the clusters into which species tend to fall are often indistinct (Fig. 1), especially when we consider fossils as well as extant species (Fig. 2), so the distinctions between taxa may not be clear and generalisations about the members of a taxon may not all apply to every species.

Evolution: branching and divergence

For many, the chief fascination of biology is that living organisms have an evolutionary history, being related to each other through descent from common ancestors. The history of life can be described by a simple branching pattern (e.g. Fig. 2) and that pattern can be reflected by the taxonomic hierarchy. Because evolution is central to biology, taxonomy has traditionally been used to summarise evolutionary relationships as well as to provide groups (clusters) about which general statements can be made. For example, as well as being seen to have many characteristics in common, species in the class Aves are recognised as sharing an evolutionary relationship closer than the relationship between any one of them and any species in other classes.

If species that were evolutionarily closely related were always more similar than those that were more distantly related, classifications could easily reflect both degrees of similarity and degrees of relationship. Unfortunately, this would only be true if evolution involved species descended from a common ancestor simply becoming steadily more and more different from each other (Fig. 3a). Unfortunately, life is not that simple: rates of divergence vary, as in Fig. 3b, in which species 3 is now

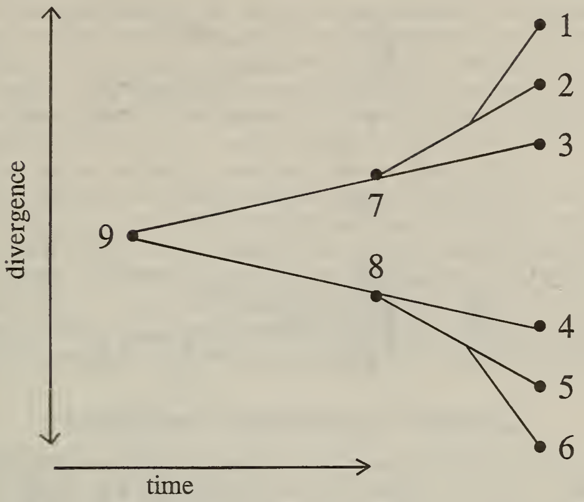

Figure 2. A hypothetical evolutionary tree in which six extant species (1–6) form two distinct clusters on the axis of divergence. The known fossils (7–9) link these clusters together.

more different from species 2 than the latter is from species 1, even though species 2 and 3 share a more recent common ancestor; convergent evolution is equally destructive of the correspondence between similarity and evolutionary relationship (Fig. 3c).

The diversity of taxonomies

Because patterns of similarity and evolutionary relationships may not be congruent and because there are various ways of describing both similarities and relationships, different taxonomists may employ different principles and procedures in their work. For the purposes of exposition, I recognise five main groups: the traditional evolutionary taxonomists, pheneticists, distance-based evolutionary taxonomists, Hennigian cladists and pattern cladists. Cladists have dominated taxonomic thinking in recent decades and some (perhaps all) of them claim that the other schools are now extinct. That this is not true is shown by the fact that the best-known recent classification of birds (Sibley & Ahlquist 1990) is distance-based. Furthermore, many non-taxonomists have grown up knowing something about traditional evolutionary taxonomy and may assume that all biological classifications rest on traditional principles and procedures. Indeed, because classifications take time to re-work, many of them still do.

It is clearly important that those who use a particular classification should know and understand the taxonomic principles used to produce it. If they do not, they are likely to draw invalid conclusions from it. The most important message I have to deliver is that it is up to the

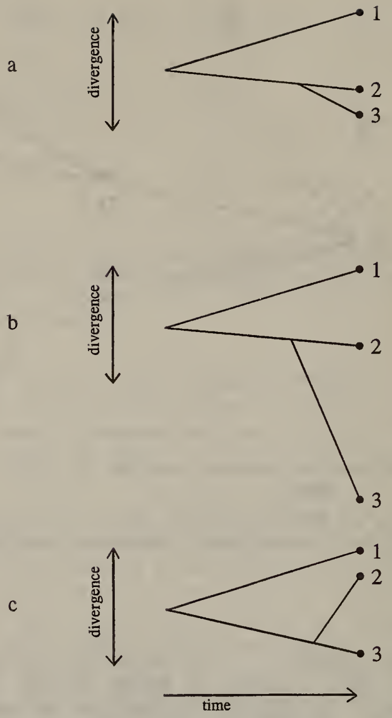

Figure 3. Three evolutionary trees. Note that each is meant to represent the actual course of evolutionary events, not what might necessarily be inferred from available evidence. In (a) species diverge at fairly steady rates, so that degrees of similarity between extant species reflect their evolutionary relationships. The correspondence between similarity and relationship is broken in (b) because rates of divergence differ and in (c) because of convergence.

taxonomist to state clearly the principles and procedures involved in producing a classification and up to the user to pay proper attention to such statements.

What sorts of characters to use?

Taxonomists differ not only in their principles and procedures but also in the sorts of characters they use as the basis for their classifications. Morphological characters have traditionally been dominant but the use of other characters has a long history: not only have naturalists long used song to identify and distinguish similar birds (e.g. White 1789) but among formal taxonomists Linnaeus (1758) used behaviour ("*adscendit noctu*", in respect of *Lumbricus terrestris*) and Nuttall (1904) used immunological characters. From time to time, individual taxonomists have promoted the use of particular sets of characters, either because of the ease with which they may be studied or because they are supposed to be particularly revealing of evolutionary relationships. The latter suppositions generally rely on questionable arguments about certain sorts of characters being evolutionarily conservative because they are likely to be less (or more!) subject to natural selection than other sorts. But, just as the history of evolutionary biology is littered with examples of characters once thought to be selectively neutral but now known to be strongly selected, so is the history of taxonomy littered with classes of characters no longer thought to be peculiarly valuable. Molecular (especially DNA) data are still often thought to be especially useful but they produce no more consistent pictures of phylogeny than do morphological data (Patterson *et al.* 1993, Sheldon & Bledsoe 1993). The best classifications are likely to result from considering all the available data—though for evolutionary and cladistic taxonomies homologous characters are of particular importance.

Traditional evolutionary taxonomy

What one regards as traditional evolutionary taxonomy is a matter of opinion. I refer to the approach, growing out of "The Modern Synthesis" of Stebbins (1950), Simpson (1961) and Mayr (1969), which has been further discussed by Cronquist (1988) and Bock (1989). It involves working out the evolutionary history of the species under consideration, taking into account evidence such as ecology and biogeography as well as the distribution of characters among species. Attention is paid to the function of characters, with assessments being made of the likelihood of different possible evolutionary changes; it is important to assess whether or not similar character states are homologous or the result of convergence. This is because taxa are required to be monophyletic which means, for the traditional evolutionary taxonomist, merely that all group members should share a common ancestor, which should also be a member of the group (Fig. 4). Note that it is not necessary that all the descendants be included for a taxon to be regarded traditionally as monophyletic, so a divergent species (or group of species) can be separated from a group with which it shares common ancestry (as taxa VI and VII are separated from taxa III and IV in Fig. 4c). For the cladist (see below), in contrast, taxa III and IV (Fig. 4b and 4c) are paraphyletic (and not allowed); strict monophyly requires that all descendants are included in the group. Thus traditional evolutionary taxonomies attempt to reflect both the branching pattern of the evolutionary trees and the extent of divergences.

The problem with traditional evolutionary taxonomy is that it is highly subjective, both at the stage of working out the underlying evolutionary narrative and at the stage of converting the phylogenetic tree into a classification.

Phenetic taxonomy

Pheneticists dispense with the subjectivity of traditional evolutionary taxonomy by abandoning the attempt to summarise evolutionary relationships in the classification. For the phenetic school, taxonomy is

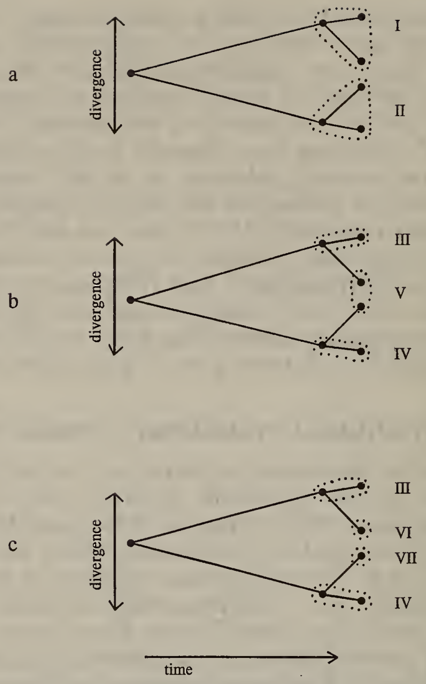

Figure 4. A hypothetical evolutionary tree and various classifications (a–c) for four extant species and two known fossils. Classification (a) would be acceptable to both traditional evolutionary taxonomists and cladists, since taxa I and II are monophyletic. Classification (b) would be more acceptable to a phenetic taxonomist, because taxon V reflects the similarity between the two species falling into it; but this taxon is polyphyletic, so the classification would be rejected by both traditional evolutionary taxonomists and cladists. The latter would also object to the paraphyletic taxa III and IV and so would also object to classification (c), though this would be acceptable to traditional evolutionary taxonomists. Whether one of the latter preferred (a) or (c) would depend on the weight he or she gave to divergence relative to phylogenetic relationship.

a matter of producing a hierarchy that reflects the inherent hierarchical clustering of nature. Species are grouped according to degrees of resemblance. In effect, species are seen as points in a multi-dimensional hyperspace, the dimensions corresponding to various characters and the positions along those dimensions being determined by how different the species are in respect of those characters. The phenetic taxonomist's job is to establish the dimensions, to measure positions and distances, and to recognise clusters (and the clusters of clusters . . .). Thus the pheneticist would apply classification (b) in Fig. 4; the fact that taxon V is polyphyletic is immaterial, since the taxa are units of resemblance not of phylogeny.

At first sight, phenetics is less subjective than traditional taxonomy because it requires no judgements about evolution. But, as Ridley (1986) and others have pointed out, it is possible to define and measure "similarity" in a variety of ways and the choice between them is entirely arbitrary; furthermore, a large variety of different methods is available for defining clusters and the choice is again arbitrary. Because the classifications produced may differ markedly according to which similarity measures and clustering methods are used, it is difficult to argue that phenetic methods are superior to traditional methods.

Distance-based evolutionary taxonomy

The extent to which single-strand DNA from two different sources produces hybrid double strands under specified conditions depends on the extent to which the two DNAs contain identical sequences, so such hybridization provides a measure of similarity. If it were true that evolution at the level of DNA (base substitution) proceeded in a steady, undirected, clock-like manner and provided that one could properly correct for the likely occurrence of changes that limit divergence (parallel changes in the two species and multiple changes, including reversals, at single nucleotide sites), then the similarity between species would reflect their evolutionary relationship (as in Fig. 3a). An essentially phenetic classification based simply on the degree of resemblance (of DNAs) would then have an evolutionary interpretation. However, the speed at which the "molecular clock" runs is clearly far from constant (Hillis & Moritz 1990) and the corrections required for parallelism, multiple hits and reversals are based on somewhat arbitrary assumptions. Furthermore, distance measures based on DNA–DNA hybridization are subject to considerable experimental error (Werman *et al.* 1990). It is for these reasons and others that the classification of Sibley & Ahlquist (1990) aroused so much controversy (see Sheldon & Bledsoe 1993, Harshman 1994). It has, nonetheless, become widely accepted, as have other classifications based on the idea that the degree of similarity (especially of DNAs) can be used as a direct assessment of evolutionary relationships.

Hennigian cladistics

Hennig (1950, 1966) revolutionised systematics by proposing clear, non-arbitrary methods for exposing the patterns of diversity that result from phylogenetic branching and for describing those patterns in an hierarchical classification. Both Ridley (1986) and Forey *et al.* (1992) present clear introductions to cladistic methods. Forey *et al.* describe its axioms as:

1. Nature's hierarchy is discoverable and effectively represented by a branching diagram.
2. Characters change their status at different hierarchical levels. Characters within a study group that are either present in all members of the study group or have a wider distribution than the study group (plesiomorphies) cannot indicate relationships within the study group.
3. Character congruence is the decisive criterion for distinguishing homology (synapomorphy) from non-homology (homoplasy).
4. The principle of parsimony maximises character congruence.

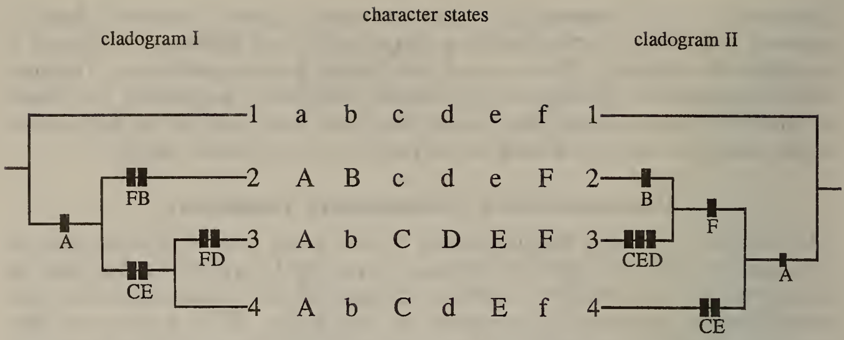

Figure 5. Two alternative cladograms for species 2, 3 and 4, based on six characters, for which the primitive states (seen in the 'outgroup' species 1) are represented by lower case letters and derived states by upper case letters. The dark bars represent points at which a primitive state changes to a derived state. Redrawn from Forey *et al.* (1992).

The branching diagrams produced by cladistic methods are referred to as cladograms. By "character congruence" is meant the co-occurrence of characters, such that they specify the same taxonomic group. Thus in cladogram I of Fig. 5, C and E are congruent (since they both occur in, and only in, the group 3–4) whereas F is incongruent with them (since it occurs not only in some, but only some, members of the group but also outside the group). Incongruencies imply convergent evolution. Cladogram II has fewer congruencies and more incongruencies than cladogram I, entailing more evolutionary changes and more convergences. By the principle of parsimony, cladogram I is preferred over cladogram II.

The stark clarity of cladistics is a recommendation in itself. Furthermore, it allows not only the process of cladogram building to be computerised but also the ready search for, and objective comparison of, alternative cladograms. Cladistics is not, however, completely objective and non-arbitrary: the taxonomist's judgment is important in defining characters and judging homology, in particular. The comparison of DNA sequences shows this up most starkly. Because sequences evolve both by substitutions of one nucleotide by another and by changes in number of nucleotides (by deletion or insertion), there are often various ways of explaining differences between homologous sequences, depending on the numbers of substitutions and deletions/insertions assumed; parsimony cannot fully resolve such cases because it is usually impossible simultaneously to minimise the number of substitutions assumed and to minimise the number of deletions and insertions.

Traditional evolutionary taxonomists have a more fundamental objection to cladistics than simply that it is not as objective in practice as it is in principle. This is that cladograms do not reflect the underlying evolutionary tree in the way that the traditionalists would like them to do. The problem lies with the cladists' rejection of paraphyletic groups, i.e. taxa which do not contain all the descendants of the common ancestor, such as taxon III in Fig. 4. One manifestation of the problem arises from traditional classifications attempting to show patterns of divergence as well as patterns of branching whereas cladistic classifications are concerned only with branching. For example, traditionalists separate the Class Aves from the Class Reptilia because of the great divergence of birds from reptiles, whereas cladists do not allow this because birds are descendants of the common ancestor of reptiles (indeed, they are, in branching terms, more closely related to crocodiles than either is to turtles or to lizards and snakes). Which classification better represents the evolutionary tree depends on one's view of the relative importance of branching and divergence. The second manifestation of the paraphyly problem is illustrated by Fig. 5, in which species 1 shows the primitive condition for all characters. Thus, on the evidence available, the most parsimonious view of the evolution of the four species in the Figure is that species 1 is the common ancestor of all of the others. However, cladistics involves recognising groups by homologies and has no means of distinguishing ancestor–descendant relationships. (Cladists would, indeed, argue that no-one has such means since, even if species 1 was represented in the fossil record at a time compatible with its being the ancestor of the others, there is no way of knowing that the fossil specimens were certainly ancestral to the other species.) Furthermore, to recognise species 1 in Fig. 5 as the ancestor of the other species would make that species itself a paraphyletic taxon, since it does not contain all its descendants. A practical example, if one assumes *Archaeopteryx* to represent the ancestor of all later birds, is that *Archaeopteryx* cannot be recognised (in a cladistic classification) as a genus equivalent to other avian genera, because it would then be a paraphyletic taxon. Cladists have attempted to resolve this problem in various ways, though none of the solutions produce classifications that non-specialists find easy to understand. Whether the matter will be resolved by non-specialists becoming sufficiently educated to be able to understand such classifications or by the partial acceptance of paraphyletic taxa, I am reluctant to predict.

Pattern cladistics

Pattern cladistics uses cladistic methods to produce classifications but it avoids the uncertainties involved in working out phylogenetic trees and the problems that arise if one tries to describe trees through classifications by ignoring evolution (for the purposes of classification). In brief, it concentrates on the pattern of organic diversity rather than on the process that produces the pattern. Ridley (1986) has argued that, once evolution is abandoned, there is no justification for cladism (it is reduced to just one arbitrary method among many for pigeon-holing animals and plants) but pattern cladists would reply that, to study evolution, one should describe the patterns first (without preconceptions) and then worry about the processes. They remain the major force in modern taxonomy and their methods have undoubtedly been useful in many systematic and biogeographical studies.

Topics addressed in the symposium

Endler (1989), in a balanced and illuminating review, has pointed out that not only is there a variety of different species concepts but that there are several major differences in the aims of species concepts and that different concepts have different uses. Much attention at the symposium, led particularly by Liversidge, by Zink and by Snow, focused on the relative merits of various species concepts, especially the *biological* and the *phylogenetic* species concepts. The latter, though it comes in various forms (see Cracraft 1983, 1989, McKitrick & Zink 1988, Nelson 1989), can be seen as a logical extension of cladistics to the species level, with its concentration on pattern rather than process. There is no doubt that, because of uncertainties associated with assessing the 'process' (potential interbreeding), defining biological species is not always easy or objective. Indeed, most evolutionary biologists would agree with Templeton (1989) that his "cohesion species concept" is generally more useful than the traditional biological ("isolation") species concept; but this still emphasises process rather than pattern. The phylogenetic concept may appear to resolve problems by concentrating on pattern but some of us remain to be convinced that it will prove more workable in practice. Indeed, disputes over trinomials (discussed at the symposium by Violani & Barbagli) are symptomatic of the difficulties of defining taxa at levels below that of the biological species. The well-known difficulties for the biological species concept of deciding whether or not to treat allopatric forms as separate species are paralleled for the phylogenetic species concept: if one applies the usual criterion under this concept that the two populations are to be specifically separated if they are diagnosably distinct, then one would separate two populations that differed at only a single genetic locus provided that difference was consistent; this would not generally be helpful, but the alternative is to impose an arbitrary rule about how much difference is required before one treats two forms as separate species—just as when applying the biological species concept to allopatric forms.

Which species concept one uses clearly has implications beyond systematics (some being explored at the symposium by Knox and by Collar) but in my view the critical points are ones that centre on systematics itself. Firstly, even though the process of speciation is usually gradual and not always a simple branching, the stage at which the genetic and ecological cohesion of a species breaks down to produce two or more separate daughter species (themselves internally cohesive) represents an important discontinuity; the separation itself favours more rapid genetic and ecological divergence, so there is a positive feedback. Secondly, the criterion of reproductive and ecological cohesion results in biological species having an objective existence in a way that other taxonomic levels do not—"the species is not an invention of taxonomists or philosophers, but it has a reality in nature" (Mayr 1988). That is why most modern philosophers of biology reject the idea that species are classes, though they may differ as to whether they are therefore to be described as individuals (see discussions in

Mayr 1988, Hoffman 1989, Sober 1993). Admittedly, this argument falls down if, like some cladists (Nelson 1989), one does not believe in species. Such extreme views should not lead us to conclude that the ideas involved in the phylogenetic species concept have nothing to offer in terms of improving our classifications. Equally, the occasional difficulties of applying the biological species concept should not lead us to abandon it, given its proven value in ornithology over the last half century.

The symposium was not only concerned with taxonomic principles and the consequences of applying different species concepts. Mikhailov's presentation on egg-shell structures reminded us of the constant search for new characters needed to resolve taxonomic problems. We were reminded of the intimate practical connection between classification and identification by Parkin's contribution on DNA-based methods for identifying individuals and their relationships and by Russell's presentation on identifying mummified falcons, where the nature of the material required the use of characters other than those normally employed.

Taxonomy is not just a subject for the specialists but a subject of importance for all biologists. The level of attendance and liveliness of debate at the symposium confirm ornithologists' current interests in avian taxonomy and the freshness of the presentations promise continuing developments of both ideas and methods.

Acknowledgements

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Species concepts

by Robert M. Zink

It is difficult to imagine a concept that impinges on more biological research than that of the species. Most biological studies refer to their subjects as members of some species (Hauser 1987). We are often taught that species are the only units in the classificatory scheme that exist independent of taxonomists; i.e. species are real. Given the importance of species in theories about evolution, ecology, and behaviour, faunal lists, and for communication of our understanding of biodiversity, lack of agreement about how biologists define species is surprising.

The species debate was evident in Darwin's time (1859), and has escaped general resolution in the last 130 years, except perhaps for the fact that most agree that the word species derives from Latin meaning 'appearance' with a secondary meaning 'kind'. Today the literature is replete with different definitions (Table 1). Some (e.g. Endler 1989) suggest that different species concepts are needed to study different evolutionary processes. Paleontologists must cope with incomplete fossil histories and absence of information on mating tendencies (Wiley 1978). Botanists must deal with reticulation, recognizing that a large percentage of all plant species, perhaps 50% or more, is of hybrid origin (Cronquist 1978). A large number of biologists claim to follow the so-called biological species concept (BSC; Mayr 1942), in which reproductive isolation is viewed as the crux of speciation. In the past 15 years, those coming from a background in phylogenetic systematics, or 'cladistics', have made substantial contributions to the debate about species, and have penned a number of 'phylogenetic' species concepts (Cracraft 1983, de Queiroz & Donoghue 1988, Nixon & Wheeler 1990). Although argument over species concepts has persisted for more than 100 years, it is my thesis in this paper that the contributions from phylogenetic systematics have substantively changed the nature of the debate. Furthermore, it is my opinion that the long-entrenched biological species concept is losing favour in ornithology (Zink & McKitrick 1995, Hazevoet 1996) and elsewhere (Mallet 1995).

Comparison of the species concepts given in Table 1 is beyond the scope of this review. Instead, I will contrast the biological species concept and a phylogenetic alternative. The reason for doing so is that I believe that the current debate about species concepts has come to focus on whether to give primary emphasis to a process, such as mate choice, or to correct representation of evolutionary patterns, such as those recovered by direct analysis of characters (Graybeal 1995). These two conceptual positions are embodied in the BSC and a PSC, respectively. Here I review each concept, noting some perceived strengths and weaknesses (Tables 2, 3).

The biological species concept has a long history in ornithology (Haffer 1992, Amadon & Short 1992, Bock 1986, Hauser 1987). A perceived advantage of this concept is that it is 'biological'. By

TABLE 1

Some species definitions or views on species

"No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species." (Darwin 1859)

"A species is a set of populations capable of combining with each other but not with other similar sets of populations on the basis of affinity and co-direction in ecological specialization." (Shaposhnikov 1966)

"A species is a group of organisms not itself divisible by phenetic gaps resulting from concordant differences in character states (except for morphs such as those resulting from sex, caste, or age differences), but separated by such phenetic gaps from other such groups." (Michener 1970)

"We may regard as a species (a) the smallest (most homogeneous) cluster that can be recognized upon some given criterion as being distinct from other such clusters, or (b) a phenetic group of a diversity somewhat below the subgenus category, whether or not it contains distinct subclusters." (Sneath & Sokal 1973)

"Somit ist die Art als das Kollektiv von Lebewesen zu bestimmen, das gemeinsam eine ökologische Nische behauptet." (von Wahlert 1973)

"Species may then be defined as groups of phenetically similar populations that have the capability to interbreed, and share similar ecological characteristics." (Doyen & Slobodchikoff 1974)

"Species, then, are the most extensive units in the natural economy such that reproductive competition occurs among their parts." (Ghiselin 1975)

"A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from any other lineage in its range and which evolves separately from all lineages outside its range." (Van Valen 1976)

"Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means." (Cronquist 1978)

"A species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." (Wiley 1978)

"A 'species' is merely a population or group of populations defined by one or more apomorphous features, it is also the smallest natural aggregation of individuals with a specifiable geographic integrity that can be defined by any current set of analytical techniques." (Rosen 1979)

"A species is a group of animals or plants all of which are similar enough in form to be considered as minor variations of the same organism. Members of the group normally interbreed and reproduce their own kind over considerable periods of time." (Trueman 1979)

"A species is a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind." (Eldredge & Cracraft 1980)

"Species are simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters." (Nelson & Platnick 1981)

"Each species is an internally similar part of a phylogenetic tree." (Willis 1981)

"We can, therefore, regard as a species that most inclusive population of individual biparental organisms which share a common fertilization system." (Paterson 1985)

"An 'evolutionary species' is a single lineage of ancestor–descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." (Wiley 1978)

"A species is what a good taxonomist says it is." (Anon.)

TABLE 1 *continued*

"At the outset I confess a disbelief in species, as that word is commonly understood to refer to the basic taxonomic unit or to the taxonomic unit of evolution . . . There seem to be no basic taxonomic units and no particular taxonomic unit of evolution . . . and as Agassiz said in 1859 'species do not exist in nature in a different way from the higher groups'." (Nelson 1989)

". . . species as the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability." (Templeton 1989)

A species is "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)". (Nixon & Wheeler 1990)

Species "refer to groups of actually or potentially interbreeding populations isolated by intrinsic reproductive barriers from other such groups. Evidence for reproductive barriers . . . will involve concordant genetic differences among the populations involved". "Subspecies are groups of actually or potentially interbreeding populations phylogenetically distinguishable from, but reproductively compatible with, other such groups. Importantly, the evidence for phylogenetic distinction must normally come from the concordant distributions of multiple, independent, genetically based traits." (Avise & Ball 1990)

"Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." (Mayr 1942)

"A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature." (Mayr 1982)

"A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent." (Cracraft 1983)

Species are "lineages whose components (if distinguishable) are not incontrovertibly on different phylogenetic trajectories (i.e. sublineages, if distinguishable, are reproductively compatible), as long as these sublineages do not form a paraphyletic group in recovered history". "The species category . . . would represent the largest entities that *have evolved* whose parts, if distinguishable, are not likely to be on different phylogenetic trajectories." (Frost & Hillis 1990)

"if a given historical group of hybridogens is persistent and is not affecting the evolutionary trajectory of its Mendelian ancestor (as indicated by biogeography, habitat preferences, or genetic divergence), it should be considered a separate species." (Echelle 1990)

A species is the "smallest recognizable monophyletic or unresolved unit". (Donoghue 1985)

"Phylogenetic species can be delimited by a procedure (population aggregation analysis) that involves a search for fixed differences among local populations, followed by successive rounds of aggregation of populations and previously aggregated population groups that are not distinct from each other." "descent relationships among [phylogenetic species] must be hierarchic." (Davis & Nixon 1992)

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observing birds from differentiated groups that interact in sympatry, one can determine if they mate assortatively. Because we observe the birds themselves choosing mates, this is deemed 'biological'. However, there is nothing 'non-biological' about the evolution of groups of individuals, the hallmark of the PSC, and the BSC cannot make a claim to be uniquely biological. Perhaps the 'B' in 'BSC' should stand for behavioural.

TABLE 2

Perceived strengths and weaknesses of the biological species concept (see Cracraft 1983, McKitrick & Zink 1988, Zink & McKitrick 1995, Zink 1996b)

Perceived strengths
- Reproductive isolating mechanisms objective in sympatry
- Reproductive isolation=genetic closure of a lineage

Perceived weaknesses
- Amount of hybridization required for conspecifity is vague
- Stable hybrid zones are difficult to assess
- Time to fusion is potentially enormous
- Allopatric populations are judged subjectively
- Evidence of evolutionary pattern is "overruled" by actual or presumed interbreeding
- Non-historical species result because hybridization is not limited to sister taxa
- Reproductive isolation is an epiphenomenon, not a directly measured characteristic of allopatric populations

TABLE 3

Perceived strengths and weaknesses of a Phylogenetic Species Concept

Perceived strengths
- Species limits are consistent with recovered phylogenetic patterns
- Same procedures used for species limits as for higher taxonomic categories
- Based directly on character variation, not an epiphenomenon such as mate choice
- Better description of spatial patterns of biodiversity
- Produces units required by evolutionary theories and conservation biology

Perceived weaknesses
- Lower limits of species require careful study of variation
- Limits of diagnosability problematic
- Too many species will result
- Species might be too ephemeral

The crux of the BSC is that species are reproductively isolated—they have reached that stage in evolutionary divergence where members no longer recognize individuals in other species as mates, or if they do, their offspring are of reduced fitness. Conversely, taxa that are reproductively compatible, especially if they interact in sympatry and form a hybrid swarm, are considered to be conspecific. Thus, the *process* of mate choice is accorded primary significance in determining whether two taxa are to be considered one or two species. This view has intuitive appeal, although I believe that the theoretical and practical flaws with the BSC are insurmountable.

One might argue that in practice the BSC cannot be deemed of primary significance because taxonomists working with some of the most speciose groups actually do not appear to use it. It would be hard to argue (see Whittemore 1993) that botanists use the BSC when delimiting species, given the propensity of plants to hybridize. Similarly, it is doubtful if entomologists (perhaps excluding lepidopterists) use the BSC, depending instead on morphological differences to recognize most species boundaries. If botanists and entomologists do not generally apply the BSC when describing species, it follows that the bulk of the world's biodiversity is classified primarily by a non-BSC paradigm.

Controversy has surrounded the BSC since its inception (Donoghue 1985, Mallet 1995), although many believe that it has survived the tests of time (Coyne *et al.* 1988). Many problems with using the BSC are familiar (Cracraft 1983), such as the need to speculate whether allopatric populations are reproductively isolated (e.g. Thompson 1991). Zink & McKitrick (1995) reviewed how the significance of hybridization has been misconstrued by proponents of the BSC. It has been implied that hybridization might 'erase' evolved differences between two taxa. However, fusion of hybridizing taxa will likely require long time periods (Zink & McKitrick 1995). Thus, the BSC has been criticized, rightly in my opinion, for basing species limits on what might happen in the future rather than what has happened during the evolutionary past (Cracraft 1983).

The primary new criticism of the BSC to emerge from the writings of phylogenetic systematists is the recognition that reproductive isolation often does not evolve concomitantly with characters that delimit evolutionary taxa, especially in the early stages of divergence. Within many biological species we can recognize separate evolutionary groups, and analyses of their relationships can suggest a pattern that is inconsistent with the pattern of reproductive compatibility—i.e., two hybridizing taxa might not be each other's nearest relatives. A 'species' consisting of two or more groups that are not each other's nearest relatives is unacceptable to modern systematists. In systematics terms, reproductive compatibility is an ancestral condition, because individuals in the ancestral population recognized each other as mates (Rosen 1979). To use the primitive ability to hybridize (perceived in allopatry or documented in sympatry) as a grouping criterion for species limits, as the BSC requires, violates the way in which systematists unite taxa in an evolutionary manner—by possession of shared-derived (i.e. non-ancestral) characters (Rosen 1979). Species limits based on reproductive compatibility (BSC) or patterns of character variation (PSC) can conflict and lead to different species limits from the same data set (Frost & Hillis 1990) (see Fox Sparrow *Passerella iliaca* example below).

The above comments do not mean that advocates of a PSC consider reproductive isolation uninteresting or unworthy of study. Indeed, one could argue that without reproductive isolating mechanisms, the world's species diversity would be kept low because taxa could not become sympatric. Reproductive isolation is an inevitable but temporally unpredictable by-product of evolutionary divergence (McKitrick & Zink 1988). At some point in evolutionary divergence, nearly all differentiated taxa are reproductively isolated, and all reproductively isolated taxa are likely to be 'good' phylogenetic species. I suspect that all species concepts recognize reproductively isolated taxa as different species. However, between the time of the emergence of taxa on their own evolutionary trajectories (as evidenced by characters) and their eventual reproductive isolation, the pattern of reproductive compatibility is an unreliable predictor of historical relationships of taxa. Although recognizing the intrinsic importance of reproductive isolation, users of a PSC choose not to include this information in the delimitation of species (Frost & Hillis 1990). In fact, proper study of the evolution of an attribute such as reproductive isolation requires first that historical patterns among taxa are known (Brooks & McLennan 1990). The potential for non-historical groupings together with the other often-noted problems (e.g. Donoghue 1985) leads to the inevitable conclusion that the BSC should be replaced with a concept that correctly represents history.

Debate continues over how to use information on evolutionary pattern to delimit species. For example, several phylogenetic species concepts exist (Table 1). Davis & Nixon (1992) suggest that the phrase "phylogenetic species concept" is misleading because the point is to delimit terminal taxa *for* phylogenetic analysis, and they describe a process whereby phylogenetic analysis does not play a role in species delimitation. Rather, they show how morphological or molecular character evidence can be used alone to delimit species. Unlike the BSC, characters are not weighted by their presumed role in a process such as mate choice. Nonetheless, common to history-based concepts, including the evolutionary species concept (Wiley 1978), is the (1) rejection of reproductive compatibility as the primary criterion of conspecific status, and (2) recognition that species can hybridize owing to the retention of the ancestral ability to do so. In my opinion, the crux of a phylogenetic species concept is to recognize groups of individuals that have been on independent evolutionary trajectories. Evaluation of multiple characters does not allow further subdivision of such groups. That is, a PSC attempts to recognize the *status quo*—character analysis reveals groups of individuals that qualify as basal evolutionary units (Cracraft 1983, 1989). Nonetheless, ongoing debate revolves around how best to recognize history at the population level (Davis & Nixon 1992, Zink & McKitrick 1995).

Several criticisms of phylogenetic species concepts exist. Avise & Ball (1990) suggested that with modern molecular methods, each individual would be diagnosable, and might qualify as a separate phylogenetic species. Indeed, if one studied individual gene genealogies (i.e. single characters), one would likely be able to circumscribe groups of individuals on a gene-by-gene basis that are not mutually exclusive, historical entities (see Maddison 1995). One might then think they are forced to recognize individual organisms as phylogenetic species to escape the problem raised by conflicting gene genealogies. However, the opposite trend is actually true. One uses multiple (unweighted) characters and resolves conflicts by an explicit *a priori* criterion (e.g. Davis & Nixon 1992). Species limits are set where character evidence becomes maximally congruent. Some character conflicts might remain, as they do in most phylogenetic studies. Thus, rather than species being single individuals, species often will become geographically coherent groupings of individuals. Resolution of conflicting character

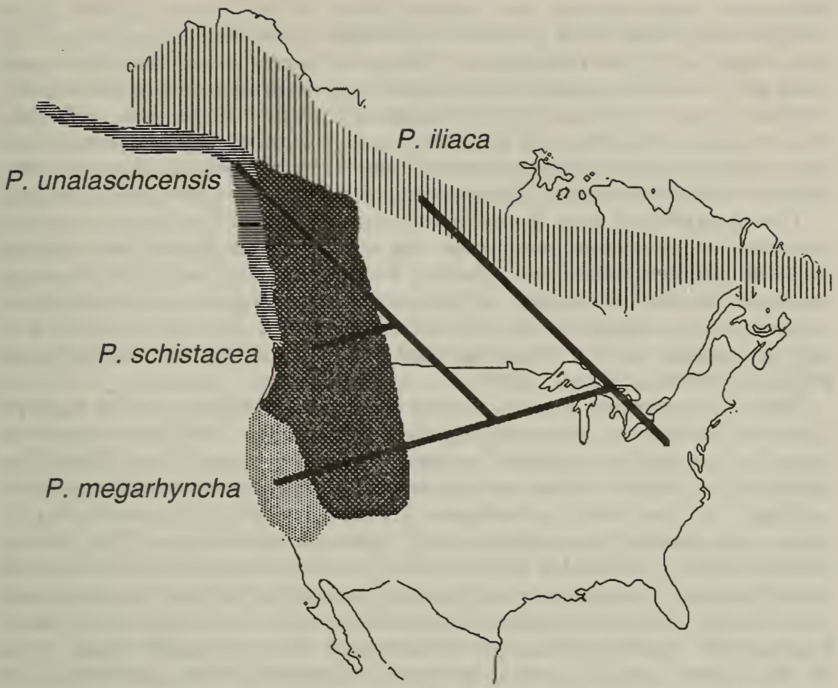

Figure 1. Approximate breeding distribution of four phylogenetic species of the Fox Sparrow *Passerella iliaca*. Phylogenetic tree derived from pattern of restriction sites (Zink 1994).

distributions (e.g. gene genealogies) results in more, not less, inclusive groupings of individuals. The mistaken belief that advocates of a phylogenetic species concept rely on single characters to delimit species has misled several authors (e.g. Amadon & Short 1992). Put another way, a problem with avian subspecies is that they are often based on single characters, and analysis of other characters can suggest different subspecific limits (see below). No taxonomic category, species or otherwise, will likely be based on single characters (Barrowclough 1982).

Differences between biological and phylogenetic species concepts are illustrated by studies of the Fox Sparrow *Passerella iliaca*. In North America, Fox Sparrows range over the taiga, northwest coast, and mountainous regions of the west (Fig. 1). There is considerable phenotypic variation, partitioned by taxonomists into 18 subspecies. However, four basic groups exist: *iliaca*, *unalaschcensis*, *megarhyncha*, and *schistacea*. Each of the four groups was originally recognized as a separate species. The Fox Sparrow is currently considered a single biological species because each group is known to hybridize with at least one other group, although only a few hybrid specimens between *iliaca* and *unalaschcensis* are known (Zink & McKitrick 1995). Zink (1994) found that each of the four groups possessed a distinct set of mitochondrial DNA haplotypes. Thus, both genetic and morphological evidence reveal four groups of individuals with separate evolutionary histories—hence, four likely phylogenetic species. (Note that molecular analysis did not indicate a greater number of taxa than that apparent from morphological comparisons.) Zink (1994) suggested, however, that further study of morphology was needed to test and refine species limits.

The question of how many biological species of Fox Sparrow exist depends on how one interprets the evidence on hybridization. An extreme view supports one species, because at least a trickle of genes links all parapatric forms. A moderate view might envisage three species, *iliaca*, *unalaschcensis*, and (*megarhyncha* plus *schistacea*). The latter grouping would obtain because of a narrow hybrid zone between the latter two taxa (Zink 1994).

The main problem in interpreting biological species limits in the Fox Sparrow concerns *megarhyncha* and *schistacea*. MtDNA evidence reveals a narrow hybrid zone between the two groups (Zink 1994). The zone seems broader when morphometric patterns are considered. The stability of the zone is unknown, a factor critical in interpreting biological species limits (Mayr 1982, Zink & McKitrick 1995). If the hybrid zone was stable, Mayr (1982) would consider *schistacea* and *megarhyncha* to represent two species because there was an unknown barrier to complete introgression despite random mating in the zone. Because the zone appears to be between two non-sister taxa, it is probably one of secondary contact (Cracraft 1989) between two phylogenetic species that have retained the primitive ability to hybridize. This study therefore illustrates the problem identified with the BSC by phylogenetic systematists (e.g. Rosen 1979); other avian examples are found in Moore *et al.* (1991) and Freeman & Zink (1995). Lumping *schistacea* and *megarhyncha* into a single species would mis-represent evolutionary history, because although they hybridize extensively, they are not each other's nearest relatives (Fig. 1). It could take tens of thousands of generations for significant introgression to occur (Zink & McKitrick 1995). The PSC would recognize the *status quo*, namely that these two taxa have had independent evolutionary histories and are therefore (phylogenetic) species. Biological species limits depend on one's interpretation of how much (or little) hybridization is required. BSC advocates could therefore recognize 1, 2, 3, or 4 species (which should challenge the belief of those who think that species are real entities of nature). However, a non-historical species including only *megarhyncha* and *schistacea*, permissible under the BSC, would be of no intrinsic value in phylogeny studies, speciation research, biogeography, comparative biology or conservation. I can think of few studies that would intentionally use this classification. Non-historical taxa, then, are the Achilles heel of the BSC.

It is worth noting that the inconsistent relationship between patterns of evolution among populations and their reproductive isolation has only recently been recognized, in part owing to molecular systematics. Molecular methods, such as DNA sequencing, can resolve evolutionary relationships over short evolutionary time scales, such as within biological species. Prior to molecular analysis, relatively little attention focused on phylogenetic relationships among, for example, subspecies (including those in the Fox Sparrow). Molecular studies can, of course, reveal taxa 'invisible' to morphologists, but more often they elucidate inter-relationships of closely related taxa. Thus, the BSC was invented and used commonly before it was realized that hybridizing taxa might not be sister taxa, and that the pattern of hybridization might misrepresent the true pattern of evolutionary history. Now, however, molecular phylogenetic analysis and classification (i.e. cladistic) methods that require taxonomic boundaries to be faithful to evolutionary ones, mean that the BSC is not an appropriate species concept.

Given the historical usage of the BSC in ornithology, one might wonder if it can be salvaged. The BSC would be improved if subspecies were phylogenetic species that were not reproductively isolated. Species would be required to be consistent with recovered patterns of history (thus, the 'Fox Sparrow' would be either one, two or four species, but one would not accept a species consisting solely of *megarhyncha* and *schistacea* given the pattern of history suggested in Fig. 1). Notwithstanding potential improvements to the BSC, 'species' would still contain variable numbers of basal evolutionary taxa, and thus not be comparable. Also species membership of allopatric subspecies would be judged subjectively, and still one would have to guess whether an allopatric taxon was reproductively isolated rather than emphasizing directly observable character variation. I think that scientific studies require more of species concepts than can be accomplished by re-modelling the BSC.

Implementation of a phylogenetic species concept would remove another contentious area from avian systematics, the subspecies category. Many practising avian taxonomists have in mind a certain 'level of distinctness' required to elevate a subspecies to species; unfortunately, this level varies from taxonomist to taxonomist because of subjective character weighting. Under a PSC, there is no need for the subspecies category (McKitrick & Zink 1988). I suggest that this would be beneficial because of the many avian subspecies that represent arbitrary divisions of clines, or are based on characters not supported by, or conflicting with, other characters. Thus, there would be a single taxonomic category for basal evolutionary taxa—phylogenetic species.

Mayr (1993) was concerned that implementation of a PSC would double the number of biological species of birds (*c.* 9000) recognized worldwide. Mayr implied that this number of species would hinder ornithological research. If this were so, botanists and entomologists surely would be unable to conduct research. G. F. Barrowclough, J. Cracraft & R. M. Zink (unpubl. data) estimated that *c.* 18,000 species of birds exist, using the PSC. This estimate was reached by evaluating morphological evidence that was gathered by previous avian taxonomists for subspecies designations; in fact, many subspecies did not qualify as phylogenetic species (see Hazevoet 1996). This number of species can hardly be perceived as a negative aspect of a PSC (Cracraft 1992). I suggest that it would (1) more accurately portray avian species diversity (Moritz 1994, Rojas 1992, Cracraft 1997), and (2) put the assessment of avian biodiversity on a more comparable footing with other groups of organisms.

Martin (1996) suggested that use of molecular methods would drastically inflate the number of avian phylogenetic species, many of which would be recognizable only with sophisticated molecular tools (i.e. beyond field identification). Zink (1996a) suggested that the number of new species that were diagnosable only through molecular analyses would in fact be relatively low, and that most taxa supported by molecular analyses also have morphological characteristics (Zink *et al.* 1995). The doubling of the number of bird species mentioned above (G. F. Barrowclough *et al.*, unpubl. data) was based solely on morphological criteria. At the Linnean symposium from which this paper derives, two independent speakers estimated the number of phylogenetic species for particular areas by examination of published (morphological) taxonomies. Thus, I doubt that molecular analyses will reveal many species that are 'invisible' to field workers (see the Fox Sparrow example above), and even if they did, would we recognize as valid components of our biodiversity only those taxa that could be identified with binoculars and a certain level of expertise?

A phylogenetic species concept would also benefit conservation biology (Cracraft 1997). Today, under the BSC, one needs to argue that sometimes local populations, subspecies, or species are units that should be targeted for conservation efforts. In my opinion, many non-systematists (and systematists) view this inconsistency as unscientific. Under a phylogenetic species concept, phylogenetic species would become the category for conservation biology. The explicit goal would be to preserve biodiversity at its most basic spatial scale. It might be thought that some phylogenetic species, formerly 'only' subspecies, would be indefensible for conservation efforts. Because conservation efforts are likely to move from the level of individual species to communities, patterns of species diversity will be used to define conservation entities, such as reserves that capture the bulk of areas of endemism. Spatial patterns of species diversity are most consistently and precisely described under a PSC.

Is the species debate important? Clearly, if different species concepts lead to different species limits given the same data, the answer is yes. The species debate is not a semantic battle between cladists and evolutionary taxonomists. Many researchers are studying speciation. If we cannot agree on a concept of species, how can speciation be effectively studied (Zink 1996b)? If we are discussing how to preserve biodiversity, and species are our measure, species concepts are extremely important. If we use species in evolutionary theories, or comparative studies (Brooks & McLennan 1990), we must be in agreement about how they are described. We must understand properties of species under differing concepts and determine that these properties are what our theories and uses of species require. Researchers should recognize the impact that different species concepts can have on their research, and explicitly consider whether their research programme depends on which concept is used.

Today, the seemingly perennial species debate has been materially changed by contributions from phylogenetic systematics, and has come to involve whether to represent evolutionary history faithfully by species limits. I think that the BSC is theoretically flawed because it can lead to, and accept, misleading historical groupings, and because there has not been a satisfactory resolution to the problem of classifying allopatric populations. Problems with a PSC involve mainly practical ones, such as how to delimit basal taxa, an impressive start at which was made by Davis & Nixon (1992). Although there will be phylogenetic species whose limits are 'fuzzy' owing to the dynamic nature of evolutionary change, and specific individuals difficult to place into a particular species, I think that these problems are far less important than the theoretical and practical ones encountered by applying the BSC. Giving primacy to correct representation of history should be the basis of our species concept, and it will produce species that are best (not perfectly) suited to the majority of biological uses to which they are put. A species concept consistent with a phylogenetic species concept should be adopted in ornithology, replacing the BSC.

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Summary

The debate over species concepts is in an active phase. After years of acceptance of the biological species concept (BSC) in ornithology and other disciplines, the field of phylogenetic systematics has contributed a significant new challenge. Reproductive isolation, the hallmark of the evolution of biological species, does not necessarily evolve in concert with characters that reflect the pattern of population subdivision. That is, taxa on independent evolutionary trajectories, only some of which might be reproductively isolated, can exist within biological species. Therefore, setting species limits consistent with patterns of reproductive compatibility can lead to species limits that misrepresent evolutionary history because hybridizing taxa might not be each other's nearest relatives. A phylogenetic species concept (PSC) equates species with groups of evolutionarily distinct groups of individuals that cannot be further subdivided by analysis of multiple characters, irrespective of mating tendencies. It requires that species limits are consistent with known patterns of evolutionary history. The PSC recognizes that (phylogenetic) species can hybridize because they retain the primitive ability to do so. The debate over species concepts currently focuses on whether to give primary emphasis to reproductive isolation and the process of mate choice (BSC), or to historical patterns of character variation (PSC); this distinction results in different species concepts leading to different species limits given the same data, such as in the example discussed of the Fox Sparrow *Passerella iliaca*. I suggest that a version of the PSC should replace the biological species concept. This would serve several useful functions, such as (1) making species of birds more equivalent with species in other major taxonomic groups, (2) providing an objective method for classifying allopatric populations, (3) removing the contentious category of subspecies, and (4) ensuring that species limits are consistent with recovered historical patterns. Fears that a PSC coupled with molecular methods would produce too many species are unfounded. The units required by phylogenetic analyses, comparative ethological, evolutionary and ecological studies, biogeography, and conservation biology are in practice phylogenetic species; biological species can fail these needs.

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Should the biological be superseded by the phylogenetic species concept?

by D. W. Snow

A controversy of fundamental importance has been developing in animal taxonomy in recent years, and is beginning to have practical effects on ornithology. It is the argument that the long-accepted biological species concept (hereafter BSC)—as expounded notably by E. Mayr in influential publications since 1942—is fundamentally flawed and should be replaced by the concept of the 'phylogenetic species'. Hazevoet's (1995) excellent check-list of the birds of the Cape Verde Islands, the latest in the B.O.U. check-list series, adopts the phylogenetic species concept (hereafter PSC), and is the first authoritative work on an entire, though small, avifauna to do so. Cracraft's (1992) reclassification of the birds-of-paradise was the first, and still remains the only, such treatment of a bird family; Livezey (1991, 1995a, b) has applied the PSC to three tribes of the Anatidae.

The principles underlying the PSC have been expounded by Cracraft (e.g. 1983, 1987, 1992), Sluys (1991) and several other authors in the U.S.A., where the concept originated; McKitrick & Zink (1988) have advocated its use in ornithology. For most British readers the most accessible, concise introduction to it will be the clear and forceful 4-page exposition by Hazevoet in Appendix 4 to his check-list.

The purpose of the present paper is not to discuss at length the arguments for and against different species concepts. This has been done in a number of publications, including those mentioned above. Its main purpose is to mention briefly what seems a fundamental weakness of the PSC; to argue that the flaws in the BSC, while not being denied, have been exaggerated; and finally to discuss in greater detail the practical difficulties that would be encountered in any attempt to apply the PSC wholesale in avian taxonomy.

The phylogenetic species

Cracraft (1983) defines a phylogenetic species as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent". Other definitions have been given, but all agree that the species should be defined as the smallest distinct group or population of common (monophyletic) ancestry; that individuals within the group must normally interbreed only with other members of their group; and that whether or not they are reproductively isolated from members of other such groups (in the sense of not interbreeding successfully with them in the event of their coming into contact) is not relevant to their species status. Species are therefore the present end-products of evolutionary change, or "evolutionary units".

It is at once obvious that, if the PSC is adopted, there will be a huge increase in the number of bird species. The species recognised will comprise every monotypic species and many of the subspecies recognised under the biological species concept. The total will increase from *c.* 9000 to perhaps 20,000 (the latter figure based largely on guesswork; many of the 27–28,000 subspecies and monotypic species estimated by Mayr & Gerloff (1994) would not be recognised as phylogenetic species—see below). One must agree with Hazevoet (1995), however, that the sheer number of species recognised under any species concept should not in itself be a factor of any importance in the argument, which is based on principle not convenience. The critical issues are two: first, whether the PSC is biologically sounder than the BSC; and second, whether its application would be practicable.

Validity of the biological species concept

The BSC is now so well entrenched in almost all standard ornithological literature that it is taken for granted by all ornithologists who are not primarily taxonomists, and by most taxonomists too. But there are difficulties in applying it, some of which are in practice insuperable. Insuperable practical difficulties do not, of course, prove that the concept is unsound. The main criticisms of the BSC—defined as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1942), with later variants which are not fundamentally different—are threefold: (1) that it is 'process-based', that is, based on an inferred speciation process, not on a rigorous analysis of taxonomically valid characters; (2) that the criterion of reproductive isolation is almost always untestable, so that informed guesses have to be made about the status of more or less closely related allopatric populations; and (3) that the polytypic species recognised under the BSC are not single irreducible evolutionary units; some (monotypic species) are, others (polytypic species) are not. Other objections that have been made seem less crucial, as they result largely from misapplication of the BSC through insufficient knowledge or inadequate analysis; for instance, that some polytypic species later turn out not to be monophyletic (with the likelihood that there are other such, not yet detected).

It cannot be denied that the first two of these major criticisms have some validity. The first is valid insofar as it reflects on the way in which some bird taxonomists have worked in the last 50 years; but as is argued below, cladistic analysis of taxonomic characters would in the great majority of cases almost certainly confirm the validity of the assemblages recognised by the BSC as polytypic species. The second criticism has long been recognised as the main stumbling block preventing a consistent and generally accepted application of the BSC. Decisions about the specific status of well-marked allopatric forms *are* somewhat arbitrary. They may even seem to be susceptible to changing fashions, as shown by the present trend towards giving species status to forms that have previously been treated as subspecies. In fact, such changes are usually a consequence of fuller knowledge of vocal differences and other potential isolating mechanisms; but see Collar

1997 (p. 130 in this issue). If the allopatric model of speciation is valid—and proponents of the PSC do not argue against it—this problem is to be expected. In any process of gradual change from one category to another there will be borderline cases; indeed it seems, as mentioned below, that the PSC encounters the same problem.

The third main criticism of the BSC is of a rather different kind. It concerns a matter of definition, and in my view is a main weakness of the PSC. It is not at once obvious why it is right to define species in the way the PSC defines them, rather than in the way the BSC does. Why, in fact, should all the distinct, even if only slightly distinct, 'end twigs' of the avian family tree be ranked as species? I know of no convincing answer. The idea seems to have a quasi-philosophical rather than a biological basis, and tends to be presented as dogma. Thus Cracraft (1992) writes: "The proper taxonomic framework for counting biological diversity resides with taxa of species rank, not with subspecies as required by the biological species concept." One is at liberty to disagree, and to answer that it is equally proper to use subspecies (as well, of course, as monotypic species). I suggest that this is a matter of opinion, not of science.

Defence of the BSC, at least in birds, can be argued more positively. Surely any ornithologist who has studied any group of birds with a wide geographical range (except perhaps some oceanic birds) must be convinced of the reality of what we have become accustomed to call 'polytypic species', however the units comprising them may be designated by taxonomists. The facts are so well known that it may seem unnecessary to labour them, but in the present context it is necessary. Typical Blackbirds *Turdus merula*—differing slightly in colour, but more in size and proportions; some very large, some very small, some of intermediate size; with rather different wing-shapes depending on whether they are migratory, resident, confined to oceanic islands, etc.—comprise an assemblage of forms which not only differ from other such assemblages but only make evolutionary sense on the assumption that they have been derived from an ancestral form probably centred on the west Palaearctic. This is an inference arrived at, not perhaps by cladistic analysis of all valid taxonomic characters (though such an analysis would almost certainly support the relatedness of the members of the assemblage), but by that generally very reliable computer, the unaided human brain. The fact that there are other more distinct, allopatric *merula*-like forms in the east Palaearctic and Oriental regions (*maximus* of the Himalayas, *mandarinus* of China, the *simillimus* group of the Indian subcontinent), and that it is impossible with present knowledge to know which, if any, of them might prove to be reproductively isolated, i.e. behave as separate species, from west Palaearctic *merula*, may be inconvenient for those wanting a stable taxonomy but is entirely consistent with the allopatric (Mayrian) model of speciation. The difficulty of deciding the taxonomic status of *merula*-like birds in the east is reasonably explained by their longer geographical isolation from western Blackbirds, and the very different environmental influences to which they have been subject and become adapted.

This kind of pattern of variation is all-pervasive; its details are summarised in regional handbooks, and dealt with in greater detail in monographs and other specialised publications. Attention is usually drawn to cases in which there is doubt as to the best taxonomic treatment under the BSC. Revisions are often made, as further data become available, but the main framework, based on the polytypic species, remains intact. It is reasonable to argue that the onus is on the advocates of the PSC to show, not only that the BSC is not a satisfactory framework for the classification of the different kinds of birds existing in the world today, but also that adoption of the PSC would be fraught with fewer problems.

Problems of the PSC

Cracraft's (1983) definition of a species has been quoted above. Nelson & Platnick (1981) give a very similar definition: "Species are simply the smallest detected samples [=populations, presumably] of self-perpetuating organisms which have unique sets of characters". In both definitions, the essential points are that they are the smallest groups of individuals and that their set of characters is diagnosable as unique. This seems simple enough, but the application of the definition would in very many cases be by no means easy. In the first place, the samples available are often not very large; in birds, their effective size would be further reduced by the need to compare specimens of the same age and sex class, and with plumage in a comparable state (breeding or non-breeding, degree of wear, etc.). Size differences may often be critical; but in passerines, for example, first-year birds are usually a little shorter-winged than older birds, and it is not always easy to distinguish them by plumage. Slight colour differences, which may be diagnostic in fresh plumage, may not be apparent in worn plumage. For the BSC, such sources of variation may make it hard to assess subspecies, but it is well understood that there may be differences of opinion about subspecies; it is not very important. For the PSC, where the decision affects the recognition or non-recognition of a species, the problem is acute. Two examples from the west Palaearctic may illustrate the kind of difficulty that will make application of the PSC hard to achieve with any hope of a consensus or of stability.

The kind of geographical variation shown by *Turdus merula* has already been mentioned. At the two extremes of size (based on male wing-length) are *T. m. maximus* of the Himalayas (144–167 mm) and *T. m. azorensis* from the Azores (117–127 mm). *T. m. maximus* should perhaps be treated as specifically distinct from the west Palaearctic forms under either of the debated species concepts; not only is it huge, but it differs quite markedly in plumage, and also in song and calls (Roberts 1992). But leaving aside *maximus*, *T. m. intermedius* of the central Asian mountains, which has typical *merula* plumage, is also very large, with a long bill, its wing-length (130–143 mm) falling outside the range of *azorensis*. *T. m. syriacus*, of Turkey and the Levant, may form a link with the European populations, being intermediate in size, but further study of these central and southwest Asian populations would be needed in order to establish how isolated they are from one another and whether variation is clinal. At the bottom end of the size range, *T. m. cabrerae* of Madeira and the Canary Islands (122–129 mm) is about as small as *azorensis*; it differs form *azorensis* in having darker female plumage, a less rounded wing, and a slightly longer tail. There is some variation within the Canary Islands, which needs further study. In Europe and North Africa, between the very large eastern continental populations and the very small Atlantic island populations, there is clinal variation which the BSC recognises by a number of subspecific names. It is generally admitted that their boundaries cannot be exactly defined (e.g. Cramp 1988).

If there is some difficulty under the BSC in deciding whether the eastern Palaearctic and Oriental groups of Blackbird-like forms should be treated as conspecific with *merula*, the problem for the PSC would involve the whole range, from the Atlantic islands to China. The Azores population would certainly be a phylogenetic species; the Madeiran and Canary Islands populations would demand detailed study. They are certainly isolated from one another and further research, including molecular analysis, would very likely bring to light diagnosable differences not only between Madeira and Canary birds but perhaps also between populations of different Canary Islands. Himalayan *maximus* and Chinese *mandarinus* would certainly be given species status, while the *simillimus* group of peninsular India and Sri Lanka would probably be treated as three species, as they comprise three rather distinct allopatric groups (5 subspecies have been recognised, but at least one pair of them intergrade). Central Asian *intermedius* might well be treated as a species, as would the main bulk of the west Palaearctic mainland populations within which variation is clinal. This clinal variation would not be given formal taxonomic recognition (see below). In fact, a major re-examination of the whole complex would be necessary before any final decision could be made on the division, into a number of phylogenetic species, of what is now treated as polytypic *Turdus merula*.

The Coal Tit *Parus ater* would present a similar, perhaps even worse, problem. It has a vast continental range in Eurasia in which variation is clinal, and a number of isolated peripheral populations, some of which are very distinct. At the extreme west of the range, *P. a. hibernicus* from Ireland is diagnosable over most of that island by a yellowish wash over its plumage, but some individuals in eastern Ireland are indistinguishable from the British population, *britannicus*, and a small proportion of birds in western Britain show a slight development of the yellow colouring that is marked in Irish birds. As British and Irish birds are not all diagnosably distinct from one another they would have to be treated as conspecific. Furthermore, the Coal Tits from the Iberian peninsula are very similar to, and in fact doubtfully distinguishable from, British Coal Tits; to the east they intergrade with nominate *ater* which extends over most of Europe and Siberia. At the eastern end of the range, there is a population in northern China very distinct from nominate *ater*, with a conspicuous crest and markedly different plumage colours (*pekinensis*). It is not isolated from nominate *ater*, but intergrades with it in Manchuria, Korea and the Amur region. Under the PSC all these populations, from Ireland and Iberia east to China, would have to be treated as conspecific, and no formal recognition would be given to their many and striking differences.

Attention would then have to be given to the isolated southern populations. They comprise what are usually recognised as 14 subspecies, ranging from northwest Africa east through central Asia to southern China and Taiwan. Some are well isolated and distinct, and would certainly be treated as phylogenetic species, e.g. *cypriotes* from Cyprus and *ptilosus* from Taiwan. Others would be problematical. For instance, the two northwest African forms, *atlas* and *ledouci*, are very distinct from all others. They differ conspicuously, but superficially, from each other, *ledouci* from mesic woodlands in Tunisia and eastern Algeria having a bright yellow wash over its plumage that is totally lacking from the very grey-plumaged, and also slightly larger, *atlas* from the Moroccan Atlas Mountains, which lives mainly in drier woodlands and at higher altitudes than *ledouci*. These two forms have stouter bills than their European relatives and differ from them in voice (Cramp & Perrins 1993). Under the PSC they would probably, at least until a short time ago, be treated as two species. There are, however, complications. It has recently been found that some populations apparently isolated in patches of rather dry montane woodland in Algeria, between *atlas* and *ledouci*, are intermediate in plumage but closer to *atlas* in size. They may constitute a third distinct form (Cramp & Perrins 1993), but have not been well studied. The Coal Tits from the Crimea, where they are well isolated from other populations, are usually considered to represent a distinct subspecies, but it is not well-marked. Further east, from the Caucasus down into the mountains of Iran, there is a trend towards brown-backed and thick-billed populations, apparently adapted to dry oak woodlands. Some at least of them are probably well isolated from others by intervening desert or semi-desert; but they have not been studied in detail and the three subspecies recognised may well need revision.

It is clear that very considerable research would be needed by anyone undertaking to reclassify the Coal Tits according to PSC principles. One can only guess at how many species would result; probably at least 15, and the number might well be altered by later research.

These examples were chosen because I happened to be familiar with them, and they may for that reason be suspected of being biased so as to exaggerate the problems of using the PSC. To check on this, I made an analysis of the 94 European breeding species in the two volumes (5 and 7) of *Birds of the Western Palearctic* containing the Blackbird and Coal Tit, using the detailed information given in the sections on geographical variation, nearly all by C. S. Roselaar. I tried to see how many phylogenetic species they would constitute and how many problems, and of what kind, would be encountered in attempting such a classification. To anticipate what is dealt with in a little more detail below, it must be noted again that the PSC gives no taxonomic recognition to geographical variation within continuous populations, however well marked it may be; all distinct and isolated populations are, as we have seen, given species status. The analysis gave the following results, summarised here in broad categories because hardly any two cases are exactly alike.

No. of spp. (BSC)	*Nature of geographical variation*	*Presumed PSC treatment*
21	None or very slight (monotypic species)	Same number recognised
18	Slight; mainly or entirely clinal	Ditto; slight geog. variation ignored
4	Moderate; mainly or entirely clinal	Ditto; moderate geog. variation ignored
5	Marked; mainly or entirely clinal (e.g. *Parus montanus*)	Ditto; marked geog. variation ignored
13	Slight, mainly clinal, but with more distinct disjunct populations (e.g. *Motacilla cinerea*, *Erithacus rubecula*)	Disjunct populations recognised as species; each BSC sp. probably becoming 2–4 PSC spp. (further study needed)
8	Moderate or marked, with some disjunct populations (e.g. *Monticola solitarius*, *Turdus merula*, *Parus ater*)	Disjunct populations recognised as species; each BSC sp. probably becoming 2–*c.* 15 PSC spp. (further study needed)
12	Marked; in distinct subspecies groups, some clinal variation within groups or areas of secondary contact/intergradation (e.g. *Cercotrichas galactotes*, *Saxicola torquata*, *Parus caeruleus*, *Lanius excubitor*)	Impossible to predict, would need detailed study
13	Complex and (except in 2 cases) marked; mainly continental ranges, probably with complex evolutionary histories (e.g. *Galerida cristata*, *Motacilla flava*, *Sitta europaea*, *Remiz pendulinus*)	Ditto

The above figures indicate that about half of the species recognised under the BSC would need further study before any attempt could be made at a PSC classification; many would have to be the subject of major revisions. Such research would certainly lead to improved understanding of the assemblages of forms involved; it seems unlikely that it would lead to stability in species-level nomenclature in the coming decades.

In making this analysis, the strong impression was gained that the great majority of polytypic species recognised under the BSC, although not based on cladistic analysis, would stand up to such an analysis and be shown to be monophyletic. In a few cases, there is doubt about whether the species recognised should be split, or merged with another species, but not about their monophyly. Before the polytypic species is rejected by proponents of the PSC, I suggest that it would be desirable to subject a representative selection of widespread polytypic species (as recognised under the BSC) to cladistic analysis, rather than reject the concept wholesale because of detected errors and questionable methods previously used in avian taxonomy.

Recognition of subspecies under the PSC

It has been widely recognised that the subspecies is not an altogether satisfactory taxonomic category, mainly because (1) geographical ranges of subspecies cannot be clearly delimited in clinally varying populations; (2) there is no general agreement (though some suggestions have been made) on what degree of difference between populations should be accepted as justifying their subspecific separation; (3) it is very often impossible to decide whether or not isolated and well-marked subspecies should be given specific rank. Means have been suggested for dealing with these problems—e.g. Huxley's (1938) notation for clines; the use of special terms such as semi-species or megasubspecies for very distinct forms thought to be verging towards specific status—but they have not been generally adopted. Lack (1968) and later authors have concluded that the objections are so serious that the subspecific terminology at present in use has outlived its usefulness and should be replaced by some more appropriate method of categorising variation below the species level.

Under the PSC, the subspecies at present has a shadowy existence in a kind of limbo. In his general, theoretical discussion of the phylogenetic species, Cracraft (1987) mentions subspecies only in a footnote, which is devoted mainly to the problems discussed above and implies that the naming of subspecies would have no place in the PSC. In his re-classification of the birds-of-paradise (1992), he is more explicit, but still with some ambivalence: "Adoption of the phylogenetic species concept solves a long-standing source of contention within systematics, namely the taxonomic status of subspecies. Because phylogenetic species are basal (smallest recognizable) differentiated taxonomic units, subspecies could only be applied as arbitrary descriptors of within-species variation. Within that context, therefore, they serve little useful purpose." In his Cape Verde Islands check-list Hazevoet (1995), after summarising the subspecies problem, concludes that "trinomials can perhaps still serve a minor role within a continuum showing clinal or otherwise geographical variation", but whenever he uses it he places the word subspecies in inverted commas, implying non-recognition of it as a valid taxonomy category.

Both authors therefore recognise the existence of geographical variation within the phylogenetic species, but decide that it does not need formal taxonomic recognition. Under the BSC, some kind of formal recognition of within-species variation is clearly essential, and the subspecies, for all its shortcomings, is the only method that has found widespread, though not uncritical, acceptance. If the PSC were brought into general use there would surely be a need, in formal listings of bird species, to draw attention in some way to clinal variation, in which differences between ends of a cline may be as marked as, or in some cases considerably greater than, differences between taxa that would rank as species. Would it be sensible, for example, to give no formal recognition to the striking difference between the small, dark, brownish Willow Tits *Parus montanus* of lowland western Europe and the large, very pale, greyish populations of eastern Siberia, because they are connected by a range of intermediate forms?

Use of the PSC in check-lists

Systematic listing of the avifauna of the Cape Verde Islands (Hazevoet 1995), with comparatively few breeding species, is not very much affected by the choice of species concept. Hazevoet recognises 14 "diagnosably distinct endemic taxa", which he treats as phylogenetic species. Four of them (*Apus alexandri*, *Alauda razae*, *Acrocephalus brevipennis*, *Passer iagoensis*) are distinct enough to be treated as endemic species in *Birds of the Western Palearctic*, the latest standard work covering the Cape Verdes. Three of the remaining 10 are oceanic birds (*Pterodroma*, *Calonectris*, *Puffinus* spp.), which present their own problems of classification; see, for example, Shirihai *et al.* (1995) on the *Puffinus assimilis/lherminieri* complex. The remaining 7 land-birds include such forms as *Buteo* (*b.*) *bannermani*, *Tyto* (*a.*) *detorta* and *Falco* (*p.*) *madens*, which under the BSC are currently treated as well-marked subspecies.

Hazevoet lists 8 "taxa of which the Cape Verde population has been treated as a 'subspecies', which is, however, not diagnostically distinct". Some of these are certainly very poor subspecies; he synonymises them with their respective continental species. But among them is the Grey-headed Kingfisher *Halcyon leucocephala*, which differs to a certain extent in coloration and measurements (especially bill-length in which there is little overlap) from its Afrotropical relatives. It is resident, having lost the migratory habit of the mainland populations. Using traditional methods of diagnosis based on measurements and plumage, and confining comparisons to adult specimens in fresh plumage, it seems quite likely that it would prove to be diagnosably distinct. Molecular analysis might be expected to support the distinction. In passing it may be suggested that it was by good fortune that the other 7 Cape Verde land-bird subspecies all proved to be poor ones; applying the PSC to some other island avifaunas might have been trickier.

A case like this suggests that proponents of the PSC, when listing local avifaunas, will be confronted with problems similar to those that face the conventional BSC taxonomist; but for the former the judgment is about the existence or otherwise of a species, and a mistake is more serious.

Application of the PSC to an inadequately known family

Cracraft's (1988) re-classification of the birds-of-paradise highlights some of the difficulties of applying the PSC to a family in which ranges and geographical variation are incompletely known. His analysis results in the recognition of 90 species, double the number recognised under the BSC (40, Mayr 1962; 42, Gilliard 1969; 45, Sibley & Monroe 1990). The increase in number of species comes mainly from the elevation to species rank of a large number of BSC subspecies.

Such a procedure is unjustified in the present state of knowledge. The collection and taxonomic study of birds in New Guinea to date involves a tiny fraction of the area of the island. In many cases nothing is known of the possible presence, or variation, of populations between the places where forms usually treated as subspecies have been collected. There may well be continuous populations, with intergradation; in such cases two or more phylogenetic species would have to be merged. Conversely, as Cracraft notes, further collecting may reveal new forms, which would be given species status under the PSC if their allopatric status vis-à-vis closely related forms could not on available evidence be disproved. In all such cases the mistakes that may result from inadequate knowledge are more serious for the PSC than for the BSC. For instance, Cracraft recognises three species of *Paradigalla*. A recent thorough analysis of this little known genus (Frith & Frith 1997) has shown that one of the three, a controversial BSC subspecies based on few specimens, is in fact indistinguishable from one of the two other (clearly diagnosably distinct) forms. The three PSC species should be reduced to two; under the BSC, the only change necessary is to reject one doubtful subspecies.

Cracraft's treatment seems in some cases inconsistent with PSC principles, probably because subjective judgment still seems necessary in spite of professions of rigorous analysis. Thus the two populations of *Lycocorax pyrrhopterus*, on Batjan and Halmahera, seem from his account to be diagnosably distinct; but he does not treat them as two phylogenetic species. The reason ("These two populations are united here until further information is available as to the extent of their behavioural and genetic differentiation") surely applies equally to forms that he does treat as separate phylogenetic species.

One result of elevating to species rank very similar subspecies of one species within a genus, such as the four forms of *Paradisaea minor*, is that the resulting genus consists of some very distinct and some all-but-identical species. There is then an obvious need to recognise a category intermediate between the phylogenetic species and the genus, as Cracraft does by placing the four above-mentioned forms in a 'species group'. This is likely to be a common problem for the PSC. If species groups of this sort are formally recognised, the arrangement that will result is likely to parallel, and in many cases become identical with, the BSC arrangement of polytypic species and their component subspecies; the PSC would simply have elevated each category to a higher rank. And all this would be due to what seems to me to be a dogma rather than a reasoned decision, that species *must* be the smallest diagnosable clusters or end-products of the evolutionary tree.

Conclusion

The arguments set out above lead, I suggest, to the conclusion that the biological species concept, while not perfect, is still useful and meaningful; and that adoption of the phylogenetic species concept is likely to be beset by problems that are equally or more intractable; at the very least, they will require years of research in order to establish which taxa, now treated as subspecies, have uniquely diagnosable characters. Even if this could be done, there would be the risk that future research and analysis, using more sophisticated methods, might necessitate constant changes. Examples of this are in fact already apparent in recent publications. Thus, in their analysis of genetic and phenotypic differences between related bird populations on either side of the Bering Strait, Zink *et al.* (1995) find that, on the basis of their DNA, the populations of *Anthus rubescens* would be considered different phylogenetic species, but no morphological differences are detectable. For some reason they do not do so on the basis of DNA alone (perhaps sensing that this would open the floodgates?), but write: "If morphological or other genetic differences between these populations are found, we think that they should be treated as separate species". How many other such cases are there which may come to light; and how many that will not come to light? From a purely practical point of view, the adoption of the PSC would mark the end of the relative taxonomic stability that has been achieved by the acceptance of the biological species concept. From a theoretical point of view, its adoption would not, in my opinion, signal any advance in our understanding of evolutionary processes at the species level.

Summary

The biological species concept (BSC), which has been generally accepted as the basis of avian taxonomy for over 50 years, has recently been challenged as being fundamentally flawed, and the proposal has been made that it should be replaced by the phylogenetic species concept (PSC). Under the PSC, polytypic species are not recognised, the species being defined as the smallest diagnosably distinct cluster or population of individuals that normally interbreed only among themselves. Reclassification of birds on PSC principles would at least double the number of species, but this is not a reason to reject it.

It is argued here that the concept of the polytypic species is based on recognition of a real and widespread phenomenon, and is not invalidated by the old-fashioned and inadequate methods that have often been used in its study. The problems encountered are just those that would be expected. It is also argued that the definition of what constitutes a species under the PSC is arbitrary and includes an element of dogma, and has no more inherent validity than definitions based on the BSC.

Wholesale application of the PSC to birds would meet with serious problems. There are many polytypic species (as recognised by the BSC) in which much further, and difficult, research would be needed if they were to be reclassified according to PSC principles, decisions about what is or is not a diagnosably distinct population being impossible on present knowledge. Even if this were done, there would always be the likelihood that further research would entail further changes. All such changes under the PSC would involve changes in the number of species recognised, and so are more serious than changes under the BSC, which would usually affect the recognition of subspecies, a category well known to be subject to change. The relative stability in species-level taxonomy achieved under the BSC would be lost, certainly for decades. To judge from publications to date in which the PSC is adopted, there would still be a need for the sort of subjective judgments that have been condemned as a fundamental weakness of the BSC. It is concluded that there is at present no case for replacing the BSC by the PSC.

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Taxonomy and conservation: chicken and egg

by N. J. Collar

Taxonomy: a dying discipline in a dying world

Taxonomy precedes conservation. This is as basic as to say that language precedes education. The one is a precondition of the other. Without the formal structure of names and an agreed system of usage, there can be no understanding of what exists to be conserved. So, if taxonomy is simply the time-honoured chicken and conservation her newest-laid egg, any implied circularity in their relationship—the point about chickens and eggs being that you cannot say which came first—might appear whimsical. However, I believe there is an important sense in which that circularity—conservation engendering taxonomy no less than *vice versa*—is now a real phenomenon.

This new emphasis is a side-effect of the widely perceived "global biodiversity crisis", in which catastrophic depletion of the natural resources of our planet by entirely unsustainable and barely controlled patterns of human exploitation—"development" is an absurd word for it—is engulfing an unprecedented proportion of the world's animal and plant species in a man-made extinction spasm (Wilson 1992, May *et al.* 1995). Many (meaning millions) of these species are not yet known to science; many (meaning hundreds of thousands) are in the half-way house of knowledge between original description and a basic understanding of their habitats, biology and distributions: up to 40% of the world's 400,000 described species of beetle, for example, are still known only from their type-localities (Mawdsley & Stork 1995). The utter inadequacy of our knowledge (although of course it has always been the case that the exploration of the planet has only ever been a subset of its exploitation) is a crippling disadvantage.

Consequently there is now enormous pressure on the discipline of taxonomy, whose services have never more urgently been needed; yet in one recent calculation (Soulé 1990), made by multiplying the number of tropic-specialised systematists on earth (1500) by the number of new species each describes per year (5) and dividing the result into the anticipated number of species awaiting description (30,000,000), it transpires that on present effort we will need to wait until the year 6000 before we have names for all the planet's species. Worse, this "present effort" shows no sign of maintaining itself for the next 40 years, let alone the next 4000: 23% of teachers of systematic biology in the U.K. were 35 and under in 1980, falling to 8% in 1990 (Gaston & May 1992). Indeed in the 20-year period after 1975 the Sub-department of Ornithology at the British Museum (Natural History) lost over half its staff, and more significantly some 90% of its research capacity (R. P. Prŷs-Jones, pers. comm.). This is the institution that houses by far the greatest amount of ornithological reference material on earth, yet now employs not a single full-time in-house taxonomist and has undertaken no exploration or collecting work of any coherent description since the Mount Nimba enterprise a quarter of a century ago (see Colston & Curry-Lindahl 1986). The situation is little different in virtually all the great old natural history museums of Europe.

Ironically, although the relative (and I stress: *relative*) completeness of avian taxonomy has prevented it from adding significantly to modern museum angst over function, direction and need, the current trend (perhaps a better word is thrust) appears to be one that will only add to the time it takes for a yet more complete ornithological world picture to be composed. Conservationists, however, may not be willing to wait; and I am inclined to think that their alliance with birdwatchers—a very strong link having been forged between the two in recent years—will be at least as crucial to the advance of avian taxonomy in the next few decades as any developments within formal academic circles.

Global conservation and international birding: parallel evolution

Birds are indeed anomalous amongst major classes or their approximate equivalents in the animal and plant kingdoms for the (relatively) high degree to which their taxonomies and distributions are known. Such knowledge is not, and can never be expected to be, complete, but it is largely sufficient for the purposes of global conservation. This is in part a reflection of the relatively low total number of recognised species (under 10,000). It is also in part a reflection of the relative ease with which birds—mostly diurnal, often brightly coloured and normally very vocal—are recorded (and indeed adopted as popular objects of interest and study).

There are several important consequences for conservation. First, it is actually still possible for an organisation like BirdLife International to consider it a realistic ambition to see *all* the world's bird species saved, even if not by its own hand. Hence the repeated evaluations of threatened species in Red Data Books remain relevant, providing the stimulus and context not only for single-species initiatives but also for site-oriented programmes dealing with major areas of sympatry between such species (Collar 1996a).

Second, the latter principle—targeting areas of sympatry between the rarer species, whether technically regarded as threatened or not—can be, and has been, formally developed as the basis of more efficient conservation investment. This could only be done in a group where taxonomic and distributional knowledge was highly advanced. Thus ICBP (1992) mapped and overlaid the distributions of 2609 bird species with ranges of less than 50,000 km^2, resulting in the identification of 221 "Endemic Bird Areas" (EBAs). An important underlying theory of EBAs is that they are likely also to be areas to which other elements of biodiversity are likewise restricted; considerable evidence has been accumulated to support this assumption (Thirgood & Heath 1994, Balmford & Long 1995), which therefore means that the targeting of conservation resources on EBAs represents a considerably more practical alternative to waiting another 4000 years for the appearance of a more sophisticated and accurate data set.

Third, it has become standard for BirdLife, in various manifestations, to promote the investigation of many of these threatened species, key sites and EBAs via self-funding expeditions, individual adventurers, holidaymakers, and of course the ever-increasing numbers of in-country ornithologists and conservationists. Biological exploration, once the exclusive province of museums and run under the direction of taxonomists, has transferred to the popular realm of conservation and amateur enthusiasm. Between 1983 and 1994, BirdLife published the reports of 43 expeditions to 30 different countries which its own staff or publications had had some direct influence in developing, and stimulated at least as many more whose results have appeared elsewhere. There has of course been a concomitant growth in interest in wild birds in most countries in the world, and BirdLife itself has worked both to encourage such growth into coalitions and clubs and to harness them for conservation purposes.

On the face of it, then, bird taxonomy in the 1990s is not a major issue: the species seem largely to have been worked out, and it simply remains for their distributions to be more finely plotted. Nevertheless—without prejudicing the claim that birds are sufficiently well known for small-ranged species to identify biodiversity sites—there are hundreds upon hundreds of taxonomic questions relevant to bird conservation that remain to be answered, many of them pressingly urgent. The interesting part is that, when these questions are not being asked by conservationists, and since in Europe they virtually cannot now be asked by taxonomists, they are very commonly coming instead—often with answers as well—from *birdwatchers*.

The reason for this is, of course, that it is birdwatchers who, alongside conservationists, are in the vanguard of the new "explorers", moving round the planet long-distance by plane, short-distance by logging road, armed with sophisticated optical and tape-recording equipment, high-quality protective clothing and the latest immunisations, and backed up with technical reference material (textbooks, recordings) of a totally new level of authority. What we find is that more and more such people are coming up against current boundaries of taxonomic clarity and knowledge, and are seeking to resolve issues beyond these boundaries on the basis of their own increasing experience and expertise. They are becoming—one only has to consider the burgeoning memberships of the newly founded Oriental, Neotropical and African Bird Clubs—a new ornithological establishment.

For such fieldworkers, unallied to museums, the question of collecting does not arise. At best, mostly on expeditions, there will be mist-netting, which allows detailed descriptions, measurements and photographs to be taken. Apart from this, their notebooks are filling up with information on foraging habitat and behaviour, nest-site selection, general habits and jizz, all of which increasingly feature as evidence in the taxonomic decision-making process. Otherwise there remains photography and in particular tape-recording. Indeed, it is probably mostly in the matter of voice that this army of avian "parataxonomists", as Janzen *et al.* (1993) call them, holds the greatest influence. It is now common for birdwatchers confidently to pronounce on the presence of species on the basis of vocalisations which to the untutored ear remain indistinguishable; the rare few, starting with the late Ted Parker, have even picked out new species to science merely on this feature.

Species limits: the key issue

The area of taxonomy which most preoccupies both international birdwatchers and conservationists is that of species limits. Generic, genetic and other levels of discrimination are largely (at present) uncontroversial. The birdwatcher and the conservationist both use the species as their unit of currency, and they both therefore have a vested interest in knowing what species there are and where, and therefore ultimately *what a species is*. Their natural diffidence over playing at taxonomy, which is widely felt to be a demanding full-time specialisation, is being forced out of them by the plain unavailability of taxonomists, and perhaps also by the growing realisation that a good proportion of current taxonomic arrangements is actually the result of past amateur (and evidently not always full-time) endeavour.

Among the obstacles they face is the quality of evidence needed to justify the splitting (or indeed lumping) of species. Particularly when a form is known to be at significant risk, and if its splitting is justifiable, then the case ought never to rest simply on an unsupported opinion, and most people would probably agree with (e.g.) Dowsett & Dowsett-Lemaire (1993) and Knox (1994) that any such decisions, irrespective of conservation considerations, require publication of the evidence. This being so, there is additional pressure on the birdwatcher and the conservationist to articulate very clearly any views they wish to see taken seriously, particularly when there *are* still taxonomists, most now in the U.S.A., well qualified to judge their efforts. This is a particularly exasperating circumstance in cases where the original professional evaluations under scrutiny (mostly dating from the era of taxonomic synthesis in the first half of this century) were themselves entirely unexplained and seemingly arbitrary.

Ideally, therefore, considerable technical detail is desirable, as for example has been adduced for Anjouan Scops-owl *Otus capnodes* (Safford 1993) and Wied's Tyrant-manakin *Neopelma aurifrons* (Whitney *et al.* 1995). On the other hand, time and resources may not easily permit such work, so that the rapid articulation of an opinion, as in the case of Visayan Flowerpecker *Dicaeum haematostictum* (Brooks *et al.* 1992), or its containment in a footnote, as with the Chinchipe Spinetail *Synallaxis chinchipensis* (see Ridgely & Tudor 1994), or even indeed an assertion as flimsy and unrefereed as that for Sumatran Cochoa *Cochoa beccarii* (Collar & Andrew 1987), may have to suffice. Sibley & Monroe (1990) took the unusual step of consulting over species limits with fieldworkers, and accepted many splits merely on their say-so. This is understandable, given the high degree of competence of many birdwatchers and the increasing use of non-morphological identification features as taxonomic characters. Indeed, the great number of further seemingly merited splits, particularly in the Oriental and Pacific regions, threatens to occupy so many years in documentation that there is clearly a temptation—all the stronger if the form is threatened (though not without the danger of distracting from other, more certain priorities)—to behave in the same apparently cavalier manner as many lumpers did earlier this century.

The birdwatcher may have more immediate interest than the conservationist in splits that involve common forms. The conservationist will have a far greater interest than the birdwatcher in splits that result in significant changes in conservation status; and it is precisely because there are potentially major financial and logistical consequences that such splits should be properly documented, although this is not automatically to admit that less rigour is acceptable where conservation is not at stake—indeed, a crucial point is that all such decisions should be made as far as possible according to the same basic criteria. So it matters relatively little to the conservationist that the two subspecies of Red-fan Parrot *Deroptyus accipitrinus* either side of the Amazon might better be treated as two species (Whitney 1996), or that White-headed and Plum-crowned Parrots *Pionus seniloides* and *P. tumultuosus* might better be treated as one (O'Neill & Parker 1977). On the other hand, it matters a great deal whether the rare Andean representative *luchsi* of the abundant Monk Parakeet *Myiopsitta monachus* has a claim to species status (Lanning 1991), and that Indonesia's Yellow-crested and Australia's Sulphur-crested Cockatoos *Cacatua sulphurata* and *C. galerita* might not merit their current specific separation, particularly if a decision to lump them (the Indonesian form being threatened) were to be accompanied by one to elevate the highly distinctive *C. s. citrinocristata*, confined to the island of Sumba.

It is in particular regard to the fate of such small-island isolates and their continental equivalents that conservationists have to be at their most sensitive and disciplined, since (a) small-island isolates are intrinsically the most susceptible to extinction (King 1985), and (b) consistency in decisions over species status is essential for long-term confidence and credibility. Thus on the one hand there is pressure, for the sake of enhanced conservation interest, to allow specific status to distinctive isolates, but on the other there is the inherent inertia of established arrangements where the elevation of one subspecies cannot wisely proceed without a revision of the entire species or indeed—where patterns of subspeciation are judged to reflect biogeographic evolution—of an entire local avifauna.

Some splits, of course, are relatively simple procedures, involving no more than two taxa and with no further ramifications, as in the case of the Visayan and Mindanao Broadbills *Eurylaimus samarensis* and *E. steerii* (split by Lambert 1996) or the Bornean and Sumatran Ground-cuckoos *Carpococcyx radiatus* and *C. viridis* (split by Collar & Long 1995). The problem is less negotiable when concern focuses on forms at geographical extremities, which sometimes (owing perhaps to founder effects or unusual environmental pressures at the very edge of a species's tolerance) exhibit the most distinctive differences from parental stock, for example the curly-tailed, dull-plumaged Tablas (Philippines) race *menagei* (see Vaurie 1949)—alas, probably already extinct—of the widespread Asian Spangled Drongo *Dicrurus hottentottus*, or the dull red Sumatran race *dedemi* of the (elsewhere mainly green) Grey-headed Woodpecker *Picus canus* (see Winkler *et al.* 1995). Most problematic of all are highly distinctive forms located geographically within a suite of generally less well-marked subspecies, like the yellow and red Visayan representative *xanthocephalus* of the normally red, green, black and white Asian Greater Flameback *Chrysocolaptes lucidus*, or the small green Flores form *weberi* of the multicoloured Rainbow Lorikeet *Trichoglossus haematodus*: splitting in such cases could not easily be done without consideration of the consequences for species limits in the rest of the complex. These types of problem are challenges for those with an interest in order and hierarchy and a great deal of time to spare, which is doubtless why so many of the earliest taxonomists were aristocrats. The hard-pressed conservationist can barely spare two hours, let alone two weeks, simply on the effort to establish the taxonomic eligibility of one or two forms to join lists of threatened species.

There are also cases where the effects of taxonomic decisions are internal to the complex under review. The Bearded Tachuri *Polystictus pectoralis*, for example, has been judged a near-threatened species (Collar *et al.* 1992, 1994), an evaluation vindicated when a full assessment of the evidence was made (Collar & Wege 1995). However, the situation only holds while it is agreed that the bird's three subspecies (one Andean, one lowland north of the Amazon, and one lowland south of the Amazon) remain as such, since each subspecies, if considered separately, would satisfy the new IUCN criteria for threatened status (the Andean form may already be extinct). Collar & Wege (1995) used this circumstance to illustrate conservation's continuing dependence on taxonomic research and on museum collections of birds. In mirror-similar fashion, the New Zealand Brown Teal *Anas aucklandica* meets the new IUCN criteria as threatened only while its three races are *not* upgraded to species level (though this is a step already taken by Marchant & Higgins 1990): once they are, two of the forms move into a higher threat category than the "parent" species, while the third (the one that continues to take the name *A. aucklandica*) drops out as threatened altogether (the reasons for this are, of course, a function of the new criteria and are discussed in Collar *et al.* 1994: 19–20).

In all these cases, of course, we are dealing with a phenomenon—allopatric disjunction—with which the biological species concept, governed by the principle of reproductive incompatibility in sympatric situations, is, on its own admission, ill-equipped to deal. The best it can do in this circumstance is to invoke criteria based on certain measures of differentiation in related taxa, whether within individual species or outside them (see, e.g., Mayr & Ashlock 1991: 104–105); but frequently no such taxa exist. Illustration of the resulting variability of treatments lies in a review of birds at risk on Negros, Philippines, by Brooks *et al.* (1992). Three of the most threatened are Writh-billed Hornbill *Aceros* *(leucocephalus) waldeni*, a split recommended by an earlier authority, adopted by Sibley & Monroe (1990) and rejected by Dickinson *et al.* (1991) despite the "admittedly considerable" differences involved; White-throated Jungle-flycatcher *Rhinomyias (gularis) albigularis*, lumped by an earlier authority but split by Sibley & Monroe (1990) and Dickinson *et al.* (1991) "on the basis of its plumage differences, dependence on lowland forest and disjunct distribution"; and *Dicaeum (australe) haematostictum*, lumped by Sibley & Monroe (1990) and Dickinson *et al.* (1991) but split by Brooks *et al.* (1992) themselves on the basis of (considerable) plumage differences, unclear vocal distinctions and absence of intermediate subspecies. Here then we have one major authority (Dickinson *et al.* 1991) accepting plumage differences, allopatry and even habitat to split a species, but unwilling to employ the first two of these criteria alone in two other cases, even though the differences that mark *A. waldeni* and *D. haematostictum* from their closest relatives are arguably far more obvious than those that so distinguish *R. albigularis*.

This variability of taxonomic treatment is an almost inevitable result not only of the predispositions and principles of taxonomists themselves—in spite of Mayr's best endeavours over 60 years—but also of the patterns of their activity and interest within taxonomy, whereby their attention can be concentrated "vertically" on particular (bio-)geographic groupings (e.g. national or subregional avifaunas), and "horizontally" on particular taxonomic groupings (e.g. families, genera). The resulting grid tends to leave some groups of species well illuminated (not necessarily *elucidated*, of course) from both directions (the Neotropical ovenbirds spring to mind) while others (for example, the Oriental babblers) remain in near darkness. The disparities of standard, judgement and focus among taxonomists only really emerge when their various works, originating at many different points in space and time, are synthesised into larger geographical reviews. Indeed, the taxonomies of the less worked regional avifaunas commonly display inconsistencies based on excessive reverence for stability on the one side and overzealous innovativeness on the other. For the conservationist at the end of the twentieth century, attempting to deal evenhandedly with such unevenness can prove to be a decidedly unrewarding and lonely task.

The challenge of the phylogenetic species concept

The biological species concept (BSC), because of the inherent arbitrariness of its treatment of allopatric forms, has been greatly vilified as the source of much of this taxonomic doubt and confusion. A phylogenetic species concept (PSC), in which a species is simply measured as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent", is being promoted, with increasing insistence, as the one clinically objective system that can resolve the problem of allopatric forms (e.g. Cracraft 1983, 1992, McKitrick & Zink 1988, Hazevoet 1994, 1996, Zink & McKitrick 1995). It is moreover claimed that "because phylogenetic species are irreducible, basal taxa, the PSC provides a better tool for assessing biological diversity'' (Hazevoet 1994). Clearly, therefore, conservationists need to consider the evidence with care.

The first thing the PSC does is obviate the problem of reproductive isolation in diagnosable allopatric forms, by pronouncing them all to be species; the next thing it does is synonymise BSC trinominals representative of clines, on the basis that all clinal populations are inherently undiagnosable as separate entities. The upshot is an anticipated net increase in the total number of bird species and the effective total elimination of subspecies. It is, in essence, as simple (and, to many, as attractive) as that: the fudge and blur of the BSC disappears, and avian diversity emerges as a sanitised, standardised construct that allows equal access to all interested parties.

Sadly, however, the simplicity is illusory. The abiding difficulty of this concept is diagnosis. Hazevoet (1994) asserted that there appears to be no theoretical limit on the number of species; but this must in part be because under the PSC there appears to be no theoretical limit on the triviality of the characters used to define them. McKitrick & Zink (1988) readily accepted this:

> scrutiny of morphological, behavioral, or biochemical characters on the ''microgeographic'' level will reveal the existence of many more phylogenetic species . . . There is no theory to suggest that a trait must be of a certain quality or magnitude to provide historical information or to describe species.

On this basis they would admit species status for a population of Trumpeter Swans *Cygnus buccinator* from a ''well-circumscribed geographic region'' if appropriate levels of sampling showed that their consistent possession of ''one extra hooklet on a barb of the seventh primary'' could diagnose them as an independent evolutionary unit. Since they admit the relevance of biochemical characters here, even absolute morphological conformity is no sanctuary from the possibility of phylogenetic splitting. Cracraft (1992) likewise comments about two forms of *Manucodia*:

> Mayr . . . notes that *trobriandi* is smaller than *comrii* and indeed most specimens fall into two distinct size groups . . . There are, however, some specimens from each form that are essentially the same size. Accordingly, only one species is recognized here, but future genetic analysis may reveal that the populations are in fact different phylogenetic species.

Here he confirms that diagnosability of characters is indeed a pursuit that can draw the taxonomist well below the level of morphology. The fact that these two forms happen to *show* some differences is only incidental: biochemistry—despite deepening scepticism in some quarters over the efficacy of its methods and hence the validity of its results—may legitimately be used to establish phylogenetic species even in cases where there are no qualitative morphological indications. Hazevoet (1996) makes a similar remark about *Pterodroma feae deserta*.

The implications of all this are that many phylogenetic species run the permanent risk of representing not ''irreducible, basal taxa'' but, on the contrary, merely the point at which the search for further diagnosable characters has been abandoned. It appears, therefore, that we are dealing with a species concept which, like the one it seeks to replace and in contrast to the claims of its proponents, can offer no actual finality or stability and which, no less than its rival, has arbitrariness and subjectivity built into its fabric. Worse yet, we are being required to place our trust in its reliance on ever more specialised and inaccessible systems of analysis, and we are presumably also expected to allow another few centuries while it works its weary way through every allopatric population of bird that man can trace and scrutinise: every inshore island population of (for example) wren (various species of *Troglodytes*), every resident landbird and breeding seabird population of every oceanic island (nearly 2000 "significant" such locations listed in Dahl 1991), every montane isolate even within the same mountain range, and so on.

Running parallel is the complex issue of voice and habitat choice as characters. It is increasingly frequent for fieldworkers to suggest taxonomic revaluations on the basis of these two elements. In particular I suspect that because North America leads the world in the realm of taxonomy, and because the Americas are so dominated by suboscine passerines with their highly stereotyped (i.e. inherited, not learnt) vocalisations, the impression across the world is that voice can be trusted as a diagnosable character, even though it is well established that for the oscine passerines environment—in terms of both conspecific singing and local habitat—is a major determinant (Hunter & Krebs 1979, Payne 1983, McGregor & Thompson 1988). Thus if the Timberline Sparrow *Spizella taverneri* is allowed species status from the allopatric Brewer's Sparrow *S. breweri* (Byers *et al.* 1995) on the basis of habitat and voice only, despite its extreme morphological similarity, this clearly has implications for any number of other allopatric populations of birds which happen to display differences in these two parameters: inevitably, again, one is compelled to ask how trivial such differences might need to be, and how they might objectively be measured. (Indeed, it is time that ornithologists considered in depth the entire question of the scientific measurement of vocal difference in relation to taxonomic valuation.)

Scrutiny of an apparently intended model of practical application of the PSC—Cracraft's (1992) review of the Paradisaeidae—only compounds these uncertainties. This analysis starts with the affirmation that, in principle, phylogenetic species are 100% diagnosable, but it transpires at once that he commonly lacks the evidence to make his judgements conclusive, and thus they often stand as "postulations"; all new species, of course, may be considered hypotheses, but the sheer degree of provisionality here rather discredits the notion that "a better tool for assessing biological diversity" is in play. Notably, Cracraft's account of one of two new species his paper describes, *Phonygammus diamondi*, reveals not only the tentativeness of his divisions but also the triviality of the characters he allows in making them. In comparing it to *P. purpureoviolaceus* he finds

> the two forms are distinct in that *diamondi* has the breast and belly dark metallic blue with no or relatively little violet-purple suffusion whereas the breast and belly of

> *purpureoviolaceus* is strongly suffused with violet-purple. In addition, the lanceolate head feathers of *diamondi* are bluish green in coloration whereas those of *purpureoviolaceus* are greenish blue often with a violet-purple tinge . . . [However] two caveats are required. First, there is considerable variation within the taxonomic entity *purpureoviolaceus* and some individuals tend towards *diamondi*. One specimen of *diamondi* . . . more nearly matches some *purpureoviolaceus*. [Second] we lack sufficient material to say whether *diamondi* and *purpureoviolaceus* are really disjunct or whether variation between these areas is clinal.

These admissions hardly confirm the inherent superiority of scientific rigour in the PSC; and one's scepticism only intensifies by reference to the start of the paper, where it transpires that the number of specimens of *diamondi* used in its diagnosis was five. This—on the basis of the passage quoted—reduces its diagnosability to no more than 80%, so that it clearly fails the test of Cracraft's own criteria, and cannot conscionably qualify even as a phylogenetic species, let alone any other kind.

To query the application is not, of course, to invalidate the principles, but I think it emerges here how little the PSC differs from the BSC in depending, ultimately, on human interpretation of the evidence, which at some point inevitably requires reasoned subjectiveness. Moreover, it is, I think, legitimate to speculate on its efficacy if it performs so inconclusively in the hands of its longest-standing and most insistent proponent in ornithology. The 40–42 birds of paradise under the BSC become, in this particular exercise, anywhere between 80 and 120 under the PSC (Cracraft actually established 90, but predicted that, while some of these would prove invalid, a good proportion of 30 additional races and even some unnamed populations would in due course prove "diagnosably distinct"). Extrapolation from these figures to the global avifauna produces 20,000–30,000 species, leaving no fewer than 10,000 forms whose taxonomic status would remain unresolved. Apart from this problem, it appears that the admission of increasing levels of triviality opens up the field for allcomers to start making their own assessments; where under the BSC such parochialism would be contained by the use of subspecies, in this scenario full species can in theory be conjured out of next to nothing by next to anybody, which will be enduringly contentious, unstable and impractical.

The absence of information on linking populations, of minor significance under BSC evaluation, here emerges as crucially important to the "ontological status" (i.e. real-world existence) of a PSC species; so for continental isolates, where intervening terrain may hold intermediate populations, PSC evaluation must remain provisional and hence seriously undependable in the short to medium term. One may even ask whether biological diversity is increased or decreased if such intervening populations are found to occur: it could not, it seems to me, do anything but increase—more populations *must* mean more diversity—yet under the PSC, by its disallowing the taxonomic subdivision of clines (which the BSC often arbitrarily breaks down into several vaguely bounded subspecies), it would be most likely, curiously, to *decrease*. Conversely, the PSC is exposed to the extraordinary situation in which the man-induced extinction of all intermediate populations in a cline would permit—indeed, I think probably *require*—the diagnosis of the two polarised populations as phylogenetic species (an increase in measured biological diversity based on a decrease in actual biological diversity). There may be cases where this kind of thing is already happening, since any break in a cline of a highly sedentary species will isolate common patterns of ancestry and descent within the resulting populations. This seems an entirely inappropriate yet inescapable upshot—two species, perhaps even three or four if enough breaks are made, where recently there was one—whereas under the BSC no change would be expected or registered.

Conservation, of course, will be more affected than any other discipline by further progress of the PSC. Apart from its fundamental long-term inconclusiveness, the fact that it would inevitably be very patchy in its adoption over time, particularly while it negotiated "ontological status" within the more complex polytypic species, would cause serious inequalities in world lists, with parts determined under one species concept and parts under another. Then again, even if the switch could somehow be effected overnight, there would remain the enormous task of distinguishing the threatened species from the secure, and of coping with the sheer volume of the former. While it is true that some threatened island forms would gain new identity as PSC species, the weight of the total number of threatened phylogenetic species (not simply proportional to the number of phylogenetic species: Collar 1996b) would tend to devalue their individual status and "jam" existing priorities with an extensive array of near-lookalikes, drawing attention away from the most distinctive species (which, I think, further compromises the PSC claim to be "a better tool for assessing biological diversity"). Conservationists would then doubtless find themselves under pressure (much of it internally generated) to make some kind of higher taxonomic prioritisations, which for the most part would lead them back towards biological species limits, and which would unquestionably absorb a great deal of their very precious time and already wilting stamina.

There is at least one further operational (although not necessarily insurmountable) drawback to the PSC for conservationists. This concerns the law. For one thing, adoption of the PSC could create chaos, at least in the short term, for trade regulation. A PSC revision of a family represented on the CITES appendices by many polytypic species would, for example, provide an opportunity for traders to test the law by trapping all subspecies (now different species) other than the nominate, whose name alone would stand as the form (species) protected under the convention. Taxonomic updates in CITES take several years, and the window of opportunity would be considerable. Certain other conventions like the Bonn and Bern likewise possess no provisions for rapid taxonomic updates, so again the scope for substantial confusion and destabilisation exists; national legislation would be similarly vulnerable. As Geist (1992) observed, once names are inscribed in law taxonomists forfeit to judges the power to decide on matters relating to the definition of species and the criteria for their establishment; some unwelcome misalignments could result. Moreover, in many countries the emergence of hundreds of new species meriting protection—these would not necessarily all be *globally* threatened—might prove highly damaging to the cause of those species already stretching the capacity and budgets of national conservation agencies.

Towards a new partnership in avian taxonomy

The PSC/BSC debate matters to conservation because it has generally been standard practice for the species rather than the subspecies to be the unit of concern (as is reflected in much national and international legislation). The PSC's greater championing of island isolates and other allopatric forms has considerable appeal but, as I have sought to show here and elsewhere (Collar 1996b), because of (a) the imbalances it would make during the long haul into global application, (b) the logjam of (often near-identical) threatened species it would create, and (c) the sheer open-endedness of its operation, the PSC appears to have little to offer as a conservation tool. My guess is that, once the search for diagnosable characters goes biochemical, the entire concept will disintegrate as an intended global standard.

Nevertheless, understandable dissatisfaction with the way lumping can mask the "true" status of various forms (e.g. Whitney *et al.* 1995) requires a response. It seems to me that there are many cases where lumping was justified and some where it was not, and that the prime task is to concentrate both field and museum studies as much as possible on likely instances of the latter, and not to allow frustration with the misapplication of one concept to result in complete dependence on another. So while the exploration of unknown or recently unvisited areas is a continuing ideal of much modern field ornithology, the rechecking of "subspecies"—all well-marked (or indeed vocally distinctive) allopatric forms—for the teasing out of false polytypic amalgams is a parallel incumbency. Objective criteria by which such forms should be identified and rechecked are themselves in need of development beyond those in Mayr & Ashlock (1991): I would imagine that habitat and elevation, and perhaps even biochemistry, would normally only be used as supplementary elements, but a way must now be found formally to invest vocalisations with the same *potential* taxonomic relevance (and I repeat there are still important caveats here too) that morphology has until now exclusively enjoyed.

A second step is the greater familiarisation of dedicated amateur birdwatchers with the principles and practices of taxonomy, which is something that both taxonomists and conservationists could encourage (perhaps a cheap manual would help demythologise the subject). Such people are, after all, the representatives of a greater, more general body of nature lovers and wildlife enthusiasts to whom conservation and, to some extent at least, modern taxonomy owe their existence. The democratisation of taxonomy, through the involvement of the growing body of highly skilled field experts, would harness new forces in the rejuvenation of this most essential and basic of biological disciplines (although I should emphasise, particularly in respect of an earlier concern about next to anybody being able to conjure up phylogenetic species, that I see taxonomic democracy as a privilege and responsibility that the entire ornithological community should commit itself jealously to guard).

Third, the challenge can partly be met by considered input into national conservation strategies, which can and should involve the identification (by national agencies) of globally threatened subspecies (Collar 1987). These forms can be allotted independent attention (including investigation of taxonomic status) chiefly when they prove not to be sympatric with "endemic" or threatened species in areas such as those identified by ICBP (1992) and Wege & Long (1995), i.e. when they fail to find sanctuary within the main suite of a country's conservation target areas. Such an approach at least promotes vigilance for the more vulnerable among less differentiated forms, without compromising either the standard use of the BSC or the global priorities that result from such use.

This agenda gives a new impetus to the chicken-and-egg cycle of (expressly avian) taxonomy and conservation. Clearly it requires coordination and consistency to be effective, and in displaying these things it might make its most valuable contribution to the growth of relations between taxonomists and conservationists concerned with non-avian life-forms, where neither side can boast a distinguished track record in strategic planning to optimise the value and impact of its work (Mound & Gaston 1993, Collar 1994). Such is the weakness of both taxonomic and conservation knowledge in most of these life-forms that conflict of interests is permanently likely, especially if taxonomy becomes thought of as a service industry whose costs should be covered by conservation or at least by the sources that fund conservation. Indeed, this is already happening: cutbacks in the core budget of the former British Museum (Natural History) have already partially been offset by its eligibility to compete, in humiliating sit-up-and-beg fashion under its new downsized identity ("Natural History Museum"), for support from the "Darwin Initiative" (the British government's Earth Summit contribution towards the conservation of global biodiversity); while the recent Systematics 2000 initiative (for which see, e.g., Cracraft 1995) shows every sign of developing into a major competitor for big-time biodiversity funding elsewhere in the world.

What is needed in this situation is redoubled government support for the institutions of taxonomy (not just in the U.K. but in every country with a museum tradition) coupled with a requirement that, rather than just resuming their timeless remit to fill out tiny random areas in the global biodiversity patchwork, they select and plan out their research priorities and activities in a serious, sustained *partnership with conservationists*, to ensure adequate and representative sampling across the planet within a time-frame (the next quarter-century) to be of maximum benefit to the preservation of biological diversity. The more such initiatives are modelled on the use of manageable, relevant subsets like those used by BirdLife in its threatened and endemic species analyses, the greater the chances that taxonomy can make a genuine contribution to the process of preserving the largest possible number of the earth's current complement of animal and plant species.

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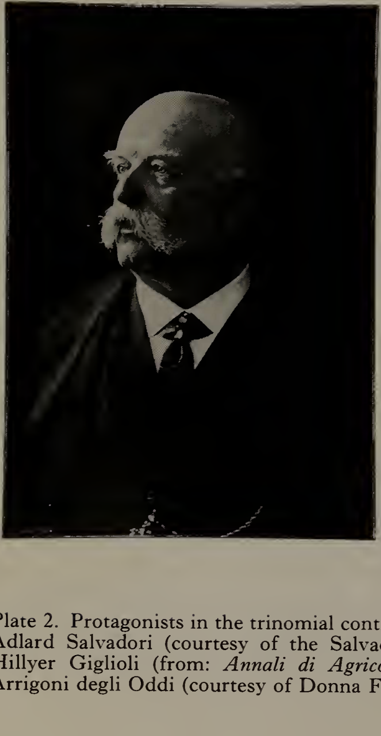

Plate 2. Protagonists in the trinomial controversy in Italian ornithology. Top: Tommaso Adlard Salvadori (courtesy of the Salvadori Muzzarelli Family). Lower left: Enrico Hillyer Giglioli (from: *Annali di Agricoltura*, no. 268, 1912). Lower right: Ettore Arrigoni degli Oddi (courtesy of Donna Fabrizia Ruffo di Calabria).

Salvadori, Giglioli and Arrigoni: aspects of the trinomial controversy in Italian ornithology

by Carlo G. Violani & Fausto Barbagli

After the publication of the 10th edition of *Systema Naturae* (1758) by Linnaeus, the adoption of his zoological nomenclature was favoured by several eminent naturalists of the 18th century in Italy, such as Giovanni Antonio Scopoli (1723–1788) and the Abbé Giovanni Ignazio Molina (1740–1829). The former, as a correspondent of Linnaeus, started using the binomial nomenclature in *Entomologia Carniolica* (1763) and, later, in 1769, as far as ornithology is concerned, in *Annus I. Historico-Naturalis*. He was the first author to describe the Little Owl *Strix noctua*, the Barn Owl *Strix alba* and the White-fronted Goose *Branta albifrons*, amongst other birds (these and other scientific names here given in their original form).

The second naturalist, Giovanni Ignazio Molina, was the librarian of the Jesuit College in Santiago de Chile; he arrived in Italy after the expulsion of the Jesuits from Chile in 1767 and lived in Bologna for the rest of his life, where he was ordained priest. In his famous essay "Saggio sulla storia naturale del Chili" (1782) he described for the first time the Chilean Flamingo *Phaenicopterus Chilensis*, the Black-necked Swan *Anas Melancorypha*, the Patagonian Kelp Goose *Anas Hybrida* and other new bird species, as well as, among mammals, the Coypu *Mus Coypus*, basing the diagnoses on his recollections. However, unlike Scopoli, Molina was not a whole- hearted supporter of Linnaeus. In the introduction of his "Saggio" he admitted:

> ". . . I have conformed to the Swedish Naturalist, not because I believe that his system is superior to all the others, but because I see that at present it is almost universally followed. Although my esteem for his knowledge is great, I cannot help saying that I do not like his very clever nomenclature in many essential points. I would have rather followed Wallerius or Bomare in Mineralogy, the great Tournefort in Botany, and Brisson in Zoology, as they seem to me easier and more appropriate for the common comprehension . . ." [transl.] (Molina 1782).

By the beginning of the 19th century, the use of binomial nomenclature was consolidated thanks to Paolo Savi (1798–1871) and Carlo Luciano Bonaparte (1803–1857). At the instigation and leadership of Prince Bonaparte, the Quarta Riunione degli Scienziati Italiani (Fourth Congress of Italian Scientists) was held in Padua in September 1842, and on this occasion the "Strickland Code" was presented to the Italian scientific community of the day, and was duly translated into Italian for the following year's meeting at Lucca. The use of the "Strickland Code", which had been successfully proposed during the Manchester Congress of the British Association for the Advancement of Science in 1842, aimed at unifying the rules of nomenclature, applying the law of priority and sanctioning any possible changes when considered necessary. The regulations fixed the 12th

Edition of Linnaeus' *Systema Naturae* (1766) as the starting point for nomenclature; the Code also had the task of preventing the kind of nomenclatural anarchy promoted by zoologists such as Illiger and Swainson (Stresemann 1975). During the following years, exploratory voyages and the systematic collecting of zoological material started the golden era of descriptive zoology, which saw Tommaso Salvadori (1835–1923) and Enrico Hillyer Giglioli (1845–1909) as its most distinguished representatives in Italian ornithology.

At Pisa University both scientists, though in slightly different times, had been pupils of Professor Paolo Savi, whose concept of nomenclature is clearly expressed in his "Ornitologia Toscana" (1827–1831):

> ". . . Names should be considered as indisputable, and they must not be changed for any reason at all; the first name which has been bestowed on a species is its true one, and it must be kept consistently and carefully; in case that the same species—due to the progress of science—needs to be placed in another genus, only then should a change in the generic name be permitted; the specific name however shall remain unchanged. . ." [transl.].

Because of their scientific influence, and the fact that they were in regular contact with the British school (Philip Lutley Sclater, Alfred Newton and Richard Bowdler Sharpe), Giglioli and Salvadori were soon considered the most authoritative ornithologists in Italy. Furthermore, Giglioli had studied at the Royal School of Mines in London and was in close contact with the cultural entourage surrounding Darwin and Huxley at the time of the great debate on the origin of species (Barbagli & Violani 1996). The work of Giglioli both as author and as museologist was based on the study of adequate series of specimens, for a better understanding of zoogeography in the light of the evolutionary theories.

In Germany the ideas of Otto Kleinschmidt, followed in Austria by Victor von Tschusi zu Schmidhoffen, and in Great Britain by Ernst Hartert, soon began to gain ground; these authors started to describe subspecies and used trinomials, whose definition was summarized by Hartert in "Vögel der Paläarktischen Fauna" (1903):

> ". . . We describe as subspecies the geographically separated forms of one and the same type, which taken together make up a species. Therefore not just a small number of differences, but differences combined with geographic separation, permit us to determine a form as subspecies, naturally when there is general agreement of the main characters . . ." [transl.].

The scientific establishment in England dominated by Sclater with Newton, Saunders, Salvin and Sharpe, was firmly opposed to such a definition and to the introduction of a trinomial nomenclature (see Stresemann 1975, Haffer 1992). In Italy too, Giglioli disagreed with Hartert, as can be seen from his famous speech delivered in 1908 in Florence, during the inauguration of the Central Collection of Italian Vertebrates; its translated quotes include:

> ". . . At this moment when a wind of analysis at all costs is blowing among the connoisseurs of natural sciences, while synthesis is either neglected or people do not know how to do it, a great danger for the descriptive and systematic aspect of science rises with the institution, let us say so, of the subspecies as new forms are being created with new

names willy-nilly more, I fear, to satisfy puerile vanity, than to establish new facts and report new cases. This, in addition to the very minute description of *individuals*, the confusion of *individual characteristics* with *specific characteristics*, is fragmenting wrongly even the common and more clearly distinguishable species, and multiplying scientific names in an incredible way; and, I am very much afraid, will lead us to total chaos . . . . If, as I always have, one accepts Darwin's grand hypothesis, one must recognize that an absolute definition of the *species* is no longer possible; what naturalist would nowadays attempt to give the *quantity* of the *species*? Nevertheless, the species exists in nature, as no one can seriously deny; but it is variable within certain limits, and is not as was once believed, a fixed and determinate entity. It is hence obvious that some species are *more* distinct, others are *less* so; the former are further removed from the congeneric species, while the latter, which are less well-defined, remain close—sometimes very close—to one or more congeneric species, being, nevertheless always detached; under normal circumstances, the former will have moved away from the ancestor species sooner than the latter. According to some, the latter hence constitute the so called *subspecies*, while others see the subspecies as a *lesser entity* lying somewhere between the species and the individual.

I would agree with the second definition, but it must be clearly stated that these subspecies are not entirely detached from the species they derive from: that is to say, some individuals will have the intermediate characteristics both of the parent species and of the new form in evolution. I could cite not a few examples of such cases; for obvious reasons, to these and these only, and even then with a great deal of circumspection, should trinomial nomenclature be applied. In my opinion the danger lies precisely in the incorrect definition of the subspecies and in the abuse of trinomial nomenclature to name the species mentioned above, which are *detached* from, but very similar to other congeneric species; therefore I use binomial nomenclature for these, since one has to be careful not to distort the grand, simple and natural Linnean concept, expressing itself in its binomial nomenclature.

. . . I would like to point out that, besides the damage due to the useless multiplication of terms, the trinomial nomenclature would necessarily imply the concept of descent, and I do not think it is easy to deduce, in most cases, which is the parent form and which the daughter. Therefore when I speak of *subspecies*, or geographical races, or *incipient* species, that is, species which are still developing, I mean the forms which have varied in a certain sense, due to the effects of the environment and of pressure from their ancestor, e.g. the species which they derive from, and they pertain to, for the presence of individuals with intermediate characteristics connecting them to that species. Since these subspecies are not yet separate from the mother species, they cannot be treated or enumerated separately, and it is only to them that trinomial nomenclature should be applied. I hope I made myself clear on this important matter. The subject deserves this. Hybrids and individual variations are, of course, a different matter, not to be confused with subspecies or incipient species, much less with the cases of neogenesis which, in my opinion, can give rise to a real and proper species, distinctly detached from its parent species. It must be remembered, furthermore, that in zoology as in the other biological sciences, nomenclature is a means, not an end. Today, the very same blessed nomenclature coined by Linnaeus to facilitate and clarify the work of the naturalist has become the greatest obstacle and the greatest source of confusion to scholars. I would add that the continual changing of the names long used up until now for common species and genera in favour of unknown or forgotten names, with the excuse of rigidly applying the law of *priority*, as well as the consequent repetition of the same name for the generic, the specific and the subspecific, has reached an intolerable paroxysm; not to mention that such puerile incongruity is revolting to even the most basic common sense. As regards myself I am also opposed to the simple repetition of the same name with generic and specific value. The enormous damage to the confusion in zoological nomenclature, to which some have even tried to make the great Linnaeus himself accomplice by using the Xth edition of *Systema Naturae* rather than the classical XIIth edition amended and corrected by himself, rightly used as the source for binomial nomenclature, prompted the discussion of a motion in section D (zoology) at the recent meeting in Dublin of the British Association for the Advancement of Science, to establish that the names in general use and which were used by the great biologists of the last century be unalterable. The proposal was therefore backed by the most illustrious British zoologists. (Cf. *Nature*, 27 August 1908). Even in the United States, where much has been committed in the name of trinomial nomenclature, last spring saw the beginning of an attempt to ward off the serious danger caused by the excessive multiplication of forms with specific value based on insufficient characteristics. (Cf. *American Naturalist*, April 1908).'' [transl.].

Elsewhere, in the last volume of his ''Inchiesta ornitologica'', Giglioli (1907) published some witty remarks, always on the same theme. Two of these, on the Corsican Nuthatch *Sitta whiteheadi* and on the Jay *Garrulus glandarius*, are particularly interesting in this respect. While dealing with *S. whiteheadi* he argued with the bird curator of the Rothschild Museum:

> ''. . . Hartert considers the *Sitta whiteheadi* as a mere subspecies of *Sitta canadensis*, to which it is doubtless remarkably similar; but in this case it seems to me that my friend has been driven by his fatherly love for subspecies.'' [transl.].

Even for the Jay, Giglioli disagreed with his transalpine colleagues; after the comparison of hundreds of specimens obtained from everywhere in Italy, he became convinced that it was a very variable species and therefore it was impossible to distinguish not only a subspecies, but even some ''local varieties'' of it. So he specified:

> ''. . . For this reason I believe it simply absurd to have separated, even subspecifically, jays collected in Sardinia from those of our mainland, as Kleinschmidt, Tschusi and—unfortunately—the able Hartert have done. And so, at a distance of one month, the former author christened his great discovery as *Garrulus ichnusae*, the latter one as *Garrulus glandarius sardus*! I feel I am watching a puerile competition on a greasy pole!. . .'' [transl.].

The thoughts of Salvadori ran along similar lines, but emerged in less emphatic tones, mainly in private documents such as his correspondence with R. B. Sharpe. In a letter dated 10th March 1904, written in a spell of low spirits, he blamed the German authors:

> ''. . . I must say that I am rather disgusted with the recent work of many ornithologists. When the trinomial system has the consequence of adopting such names as *Coccothraustes coccothraustes coccothraustes*, *Oriolus oriolus oriolus*, *Pica pica pica*, I conclude that the system is absurd! No less absurd is Hartert's system of using the names *Carpodacus* (mas.) *rhodochroa* (fem.), *C. rhodopepla*, *C. rosea*, *C. erythrina*, *C. synoica*. Sensible people will laugh at us if we continue in this way . . .'' (Violani in: Anon. 1993).

In the paper written for *The Ibis* Salvadori (1904) carried on a controversy with his friend Hartert concerning the choice of the 10th edition of Linnaeus' *Systema Naturae* as the starting point for zoological nomenclature and its consequences in the case of the Latin naming of two common species of European thrushes, *Turdus musicus* and *Turdus iliacus*.

The first Italian author of the new generation, 22 years and 32 years younger than Giglioli and Salvadori respectively, who did not oppose the trinomial nomenclature is Count Ettore Arrigoni degli Oddi (1867–1942), owner of an extraordinarily rich private collection of birds (Barbagli *et al*. 1996), and in touch with Tschusi and Hartert as a collector. He adopted trinomial nomenclature, when in 1902 he described seven subspecies of birds (five from Sardinia, one from Corsica, one from mainland Italy), thus publishing avian trinomial names for the first time in Italy (Arrigoni degli Oddi 1902a, 1902b).

Although Arrigoni degli Oddi had joined the new school as far as trinomial nomenclature was concerned and used it in his "Elenco degli uccelli italiani" (1913), in the same book he made it clear that:

> ". . . As regards subspecies, I did not omit to mention them under each single species, mostly in order to keep my work updated; as for myself in most cases I am not even able to distinguish them and I consider an analysis carried to the extremes to be a very serious damage to science. With the greatest thoughtlessness new names are given to new forms almost always based on individual, not specific, characters; in this way, such a confusion of technical names and of forms is created, that sometimes one is at a complete loss . . ." [transl.].

The same concept was taken up again in greater detail by Arrigoni degli Oddi in "Ornitologia italiana" (1929), when the author explained his objection to the contemporary significance and usage of the subspecies:

> ". . . The name "subspecies" was given, adopting trinomials, to those small variations which depend on habits, life environment, locality or other factors, emanating from a close origin, and, if not in all, consistent in their complex and to which they are connected thanks to intermediate individuals. Today, however, the subspecific distinctions multiply continuously, and in such way that they give birth to great confusions, and make scientific researches less serious. Different names were also proposed in order to indicate the various modifications undergone by the type species in the different countries, and excessively fanciful or unimportant features were fixed. "This according to myself [M. Paulucci 1879, p. 79] cannot be undertaken seriously, as these modifications pass imperceptibly from one to the other, and through innumerable tiny changes unrolls and develops a chain formed by a quantity of small links all connected together." Many of these modern distinctions were established upon a single specimen, comparing it with some similar ones from a very distant locality, without paying attention to the fact that in the intermediate countries the various links could be found, and without considering that it is with large series that species must be established. . ." [transl.].

As far as trinomial nomenclature was concerned, the controversy in Italy was a matter more of form than of content; indeed, during his studies on the Moluccan and Papuan avifaunas Salvadori did describe a *Semioptera wallacei* var. *Halmaherae*, as well as a *Paradisaea apoda* var. *novae guineae*, signifying his intention to point out morphological differences when perceptible and consistent (Salvadori & D'Albertis 1879, Salvadori 1882).

In reality, Salvadori rather often employed the term "variety" in order to indicate individual variations, as for instance *Eos riciniata* (Bechst.) var. *cauda viridi* (Salvadori 1881). In the above cases of birds of paradise, however, as is shown by the geographical names adopted and by the considerable number of syntypes examined (40 specimens of var. *novae guineae* and 50 of var. *Halmaherae*), he intended to designate two entire morphologically consistent local populations; thus he used the term "variety" in the same way as the new school of his time was using the word "subspecies". The step between "variety" and "subspecies" was short, as is apparent from the ruling of the I.C.Z.N. (1985) to consider the term "variety" as of subspecific rank, if published before 1961, unless the content of the work reveals that infrasubspecific rank is meant [Art. 45(g)].

The reluctance of Giglioli to use "subspecies" derived from the impossibility of arranging trinomials according to phylogenetic descent; consequently, he indicated as species different forms even "very little detached" from each other, on condition that all the individuals belonging to these forms could be separated on the basis of morphological characters. His belief is well expressed in a passage on the Black-eared Wheatear *Saxicola melanoleuca* (now *Oenanthe hispanica melanoleuca* Guldst.).

> ". . . The difference between these two forms [*Saxicola melanoleuca* and *S. occidentalis*] is not great, but it is constant, therefore they should be kept as distinct. According to modern criteria they must be considered as *subspecies* or incipient species, as it is better expressed; but it is not possible to tell which of the two is the more ancient, or from what ancestor the other has derived. Such a fact illustrates very clearly the fallacy of burdening the already overloaded ornithological terminology with a trinomial nomenclature. Who could prove to me in this case (and almost all the so-called subspecies are in such a condition) that it is correct to write: *Saxicola occidentalis melanoleuca* or *Saxicola melanoleuca occidentalis*, in order to distinguish the two forms; or, on the contrary, using the incongruous and monstrous repetition of the specific name in order to designate the mother form, to write: *Saxicola melanoleuca melanoleuca* or *Saxicola occidentalis occidentalis*? For obvious reasons of order and logic, I prefer to maintain the admirable and very simple binomial nomenclature of the most celebrated Linnaeus; affinities, as well as divergencies between two forms (let us call them "species"), are variable quantities and easily measured very differently by the various scholars, so that we cannot always have a sharp and precise definition to distinguish *species* from *subspecies*; still less easy is it to establish which is, between two related forms, the (mother) *species*, or the (daughter) *subspecies*; since such should be their true and phylogenetic relationships . . ." [transl.] (Giglioli 1894).

After the death of Giglioli and Salvadori, the use of trinomial nomenclature in ornithology was accepted in Italy without further controversy; Arrigoni degli Oddi used trinomials in his textbook "Ornitologia italiana" (1929), though remaining sceptical, as we have seen, to the so called "manufacturing of subspecies" by his German colleagues.

As a curiosity it may be recalled that, during the 1950s and 1960s, Antonino Trischitta (1892–1966), an eccentric Sicilian naturalist, proposed a bizarre nomenclatural system, which he called "Nomenclatura Biologica ternaria plurinominale" (Ternary plurinominal biological nomenclature). This system (Trischitta 1950, 1967) was intended to reveal the exact position of the living being, which the name referred to, within the systematic frame. The three terms indicate: the first, the kingdom, the phylum, the class and order which the organism belongs to; the second, the family and the genus included in the same family; the third, the species and, possibly, the subspecies. For instance, applying Trischitta's system the scientific name of Bonelli's Eagle would be:

Zochoaviaccipitrides accipitriihieraaetus fasciatus

resulting from:

Regnum: Animale (Zoo)	*Zo*+
Phylum: Chordata	Zo*cho*+
Classis: Aves	Zocho*avi*+
Ordo: Accipitriformes	Zochoavi*accipitrides*
Familia: Accipitridae	*accipitrii*+
Genus: Hieraaetus	accipitrii*hieraaetus*
Species: fasciatus	*fasciatus*

This method had no followers, but nevertheless it stimulated a short-lived interest and its mechanism was published in the pages of the authoritative "Bollettino di Zoologia" (Trischitta 1952) edited by the Unione Zoologica Italiana.

Summary

After the publication of Linnaeus' *Systema Naturae* (1758) binomial nomenclature was also introduced in Italy and adopted by several famous naturalists of the 18th century, such as Giovanni Antonio Scopoli and the Abbé Giovanni Ignazio Molina. By the beginning of the 19th century its use was consolidated thanks to the work of Paolo Savi and Carlo Luciano Bonaparte. Under the leadership of the latter scientist the Quarta Riunione degli Scienziati Italiani was held in Padua in September 1842 and, on this occasion, the Strickland Code, subsequently translated into Italian, was recommended since it fixed the 12th edition of *Systema Naturae* as starting point for scientific nomenclature.

Subsequently, voyages of exploration and the systematic collecting of zoological material started the golden era of descriptive zoology, which had Tommaso Salvadori (1835–1923) and Enrico Hillyer Giglioli (1845–1909) as its most distinguished representatives in Italian ornithology. Between the 19th and the 20th century the German-speaking ornithologists Ernst Hartert, Otto Kleinschmidt and Victor von Tschusi introduced the subspecies concept and began to use trinomial nomenclature consistently in their writings. In Italy this new school found an eminent supporter in Count Ettore Arrigoni degli Oddi (1867–1942), who in 1902 described his first new subspecies of Italian birds using trinomials, in conflict with the old school of Salvadori and Giglioli.

At about the same time in England a similar situation occurred, between the younger Hartert and the older ornithologists such as Richard Bowdler Sharpe, Philip Lutley Sclater and Alfred Newton. The controversy which ensued lasted for about twenty years and is still remembered thanks to private correspondence and articles in scientific periodicals by the authors involved; though sometimes extremely polemic, their tone was frequently enlivened by humour as is shown, for instance, in Giglioli's writings.

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Scopoli, Linnaeus and the Wallcreeper *Tichodroma muraria*

by Fabio Barbagli, Fausto Barbagli & Carlo Violani

While examining letters written to Carl Linnaeus (Råshult 1707–Hammarby 1778) by Giovanni Antonio Scopoli (Cavalese 1723–Pavia 1788) now preserved in the Linnean Society's Library, London, and the respective replies published by Cobelli & Delaiti (1889) and recently by Soban (1995), we found interesting details on the nomenclature of some animals including the Edible Dormouse *Myoxus glis* (Violani & Zava 1995) and the Wallcreeper *Tichodroma muraria*. This bird was not included in the tenth edition of *Systema Naturae* (1758) probably because being a species foreign to Sweden it was unfamiliar to Linnaeus. Scopoli was a faithful correspondent of Linnaeus. He was employed by the Austrian Imperial Government as a physician to the quicksilver miners of Idria in Carniola (the region around Ljubljana in Slovenia) and his salary was supplemented by the tax money collected on wine sold in the area (Scopoli 1786–1788). Although isolated, Scopoli cultivated interests in many fields of the natural history of Carniola, botanizing, collecting insects and making observations on the local birds, during a long residence in Idria and on his trips through Slovenia and Friuli.

He wanted to send a specimen and communicate first-hand details of the Wallcreeper to Linnaeus so that his Swedish correspondent could include it in a future revised edition of *Systema Naturae*. In a long letter to Linnaeus, dated 28 January 1762, Scopoli announced that he had sent a *Upupa muraria* in a box together with other scientific material. However Linnaeus was unable to find the bird in the consignment when he opened the box, and so noted down on the left margin of Scopoli's letter: "*Hanc non reperi in cistula; certe neglexit imponere Scopoli* . . . " ["I did not find this in the box; certainly Scopoli must have forgotten to put it in . . . "].

On 11 February 1762, the Italian author apologized for his negligence and wrote: " . . . *In cysta, pro Te, Cl. Gronovio missa, non invenies Picum murarium Aldrov* . . . *Nescio enim quo fato, apud me denuo remanserit, mittam tamen alia vice. Avis haec non est Picus, sed meo iudicio Upupa corpore supra cinereo, gula alba abdomine cauda alisq. nigris: basi remigibusq. primariis semirubris: tribus primis maculis duabus albis* . . . " [" . . . In the box, sent to you through the celebrated Gronovius, you will not find the *Picus murarius* of Aldrovandi . . . I do not know by what mischance it remained with me, but I will send it some other way. This bird is not a woodpecker, but in my judgement an Hoopoe, with ash grey upperparts, throat white, belly, tail and wings black with the base of the primaries half-red, the three outer ones with two white spots . . . "].

At last, with a long letter written by Scopoli on 7 April 1763, Linnaeus received a specimen of the bird accompanied by an accurate description of *Merops murarius*. Scopoli wrote: " . . . *En descriptionem*

Gliris Romanorum et Pici murarii, quibus nonnullas alias observationes adiungo. . . . Merops (murarius), cinerascens, rostro abdomine cauda alisque nigris, remigibusque primariis semicoccineis, rectricibus apice albentibus . . . Habitat et nidificat in Arcibus elatioribus et desertis, nec non in turribus . . . " ["Here is the description of the Dormouse of the Romans and of the Wallcreeper, to which I am adding some other observations . . . *Merops murarius*, ashy coloured, bill, abdomen, tail and wings black, the primaries half scarlet, the rectrices white-tipped . . . It inhabits and nests on the higher solitary fortresses, as well as on towers . . . "].

A longer, detailed description followed. This was meticulous when giving body characters, and he obviously had a freshly killed specimen in winter plumage in front of him when writing the letter, since he was able to describe the shape of the nostrils, of the tongue and of the palate. A vivid report of the Wallcreeper's behaviour revealed that Scopoli had observed the bird in life personally: "*Sub finem Autumni migrat solitarius, volatu vago, remigante, muto. Aedificia elatiora, turres et Arces adit, muris insidet, super hos saltitando reptat, fenestras et latebras recognoscit, araneas devorat, muscas segniores capit, inquietus, frigoris amans, numquam pinguescens.*" ["Towards the end of Autumn it migrates alone with a wandering, flapping, silent flight. It visits the higher buildings, towers and fortresses, sits on the walls, creeps on them hopping, explores windows and concealed places, devours spiders, catches the slower flies, restless, loving cold weather and never getting fat"].

On 17 May 1763 an enthusiastic Linnaeus replied from Uppsala, gratefully acknowledging Scopoli's helpful information: "*Epistolam tuam V. A. d. 7 aprilis data rite accepi, . . . perplacuit pulcherrima avis europaea Picus muralis dicta* . . . " ["I have safely received your letter dated 7th April, . . . I liked very much the beautiful European bird called *Picus muralis* . . . "].

Linnaeus included it as a new species under the name of *Certhia muraria* in his 12th edition of *Systema Naturae* (1766), where he acknowledged the information received. Later, Scopoli (1769) published a very similar diagnosis for *Certhia muraria*.

An interesting point concerns the type-locality of *Certhia muraria* Linnaeus 1766. Although briefly mentioning other authors, such as Gesner, Aldrovandi, Kramer and Brisson, Linnaeus clearly relied on Scopoli's contribution for the printed description of the Wallcreeper. Since Scopoli's specimen is stated to originate from Carniola, according to correspondence with Linnaeus, we believe that the Linnean type-locality ("*Habitat in Europae australis turribus, arcibus*") of *Tichodroma muraria muraria* (L.) can be restricted to Carniola in Slovenia.

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Molecular probes for identifications of raptors

by D. Parkin

Research into the Red Kite *Milvus milvus* at Nottingham resulted in the isolation of a clone DNA that is inherited in a sex-limited fashion. It reveals a multi-band profile that is transmitted *more or less* faithfully from mother to daughter. This 'matrilineal' pattern is typical for DNA that is sited on the female-specific (W) chromosome. Analysis of a series of unrelated female kites from Germany and Spain revealed that there were 20 different patterns among 27 nest sites. There was no evidence of a common pattern between the two regions.

A long series of females from Wales revealed only two profiles, suggesting that this population is distinctly less variable. This finding is supported by the analysis of multi-locus DNA profiles in kites from these three regions.

A single locus was analysed using an oligonucleotide probe. The number of alleles detected was significantly less in the birds from Wales, whereas those from Germany and Spain did not differ.

All these results suggest that Red Kites from Wales are genetically depauperate.

Interestingly, a southern isolate of the Welsh populations revealed a significant difference in genetic structure. First, the two matrilines differed in relative frequency, and second, the single locus data differed. The rarer of the matrilines was very similar to a German profile, suggesting the possibility that a bird from this region had colonised South Wales at some time close to the date of spread from the traditional range in mid-Wales.

In the late 1980s, it was decided to attempt to re-establish the Red Kite into an area of southern England from which it has been absent for over a hundred years. Blood samples were taken from the released birds which were also marked with rings and patagial (wing) tags. When breeding commenced, the identity of pairs was determined visually, and their success monitored. Blood samples taken from the nestlings permitted confirmation of identity and parentage.

Although numbers were very small, evidence suggested that birds from Wales bred later and were less successful than the main release from Spain. This supports the hypothesis that the Welsh birds are not only less variable (inbred) but also less successful (inbreeding depression). Supporting evidence will be presented, and recommendations made for future releases in any re-introduction programme.

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X-raying the Gods: what were the mummified Horus falcons of Egypt?

by D. A. Russell, B. Galeb & R. Hoath

As part of the Egyptian Exploration Society (U.K.) investigation of the social and temporal context of the Sacred Animal Necropolis at Saqqara, Egypt, in 1992, 1994 and 1995, identification to species level was attempted for some 200 mummified 'falcons'. These were amongst the hundreds of thousands deposited in underground galleries from c. 600BC to 100AD by devotees of the religious cult of Horus worship. Many of the remains were in poor condition, partly as a result of the 'hot dipping' method of mummification used and partly because of the age and condition of the material at the time of its mummification (many specimens were partial skeletons, mixed species or other material, e.g. eggshells, twigs or shrews).

Identification by manual unwrapping was both laborious and destructive, owing to the friable nature of the material, and the wrapping of some specimens was too fine to permit destructive sampling. Consequently, a sub-sample of mummies was X-rayed on site. A portable army field machine, manufactured by the Massiot Society, was operated at 10 mA and 60 kV by Drs R. and M. Lichtenberg with the kind permission of the Mission Archéologique Française du Bubasteion. Apart from the need for accurate scaling,